Notes on Atlantic Asteroidea. 2. Luidiidae

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Introduction

In reviewing the Atlantic species of Asteroidea, recent proposals for inclusion of the family Luidiidae in the order Paxillosida rather than the Platyasterida (as in the 'Treatise of Invertebrate Paleontology') need to be discussed. Also, several taxonomic complications to do with the large genus *Luidia* have become apparent, particularly in reassessing the ranks of similar taxa from the continental shelves on the two sides of the ocean. These are better disposed of in a preliminary paper.

The large collections of the *Pillsbury* and *Gerda* of the University of Miami from both sides of the tropical Atlantic have supplemented the material already in the British Museum (Natural History). Only *L. patriae* Bernasconi from Argentina is not available, so comments on its affinity with *L. scotti* Bell are based on the published description. The number of nominal species occurring in the Atlantic is reduced by synonymy or lowering to infra-specific rank from 17 to 11. Coverage of *L. atlantidea* Madsen, *L. barbadensis* Perrier, *L. ciliaris* (Philippi) and *L. senegalensis* (Lamarck), all of which are limited to either east or west, is restricted to inclusion in a tabular key of principal characters and an outline of the distribution. Also *L. clathrata* (Say) raises only a nomenclatural problem, being another species of limited range. A neotype for *L. alternata alternata* (Say) and a lectotype for *L. sarsi sarsi* (Düben & Koren) are designated and discussed.

The good size range of specimens from the Miami collections has allowed for some comments on post-metamorphosal growth changes.

Systematic account

LUIDIIDAE Sladen, 1889

Astropectinidae: Luidiinae Sladen, 1889 : 244.

Luidiidae: Verrill, 1899 : 201; Fisher, 1911 : 105; Bernasconi, 1943 : 2–3; Fell, 1963 : 433; Spencer & Wright, 1966 : U42; Downey, 1973 : 21; Blake, 1973 : 22–24 (pt); A. M. Clark & Courtman-Stock, 1976 : 43; McKnight, 1977 : 116; Blake, 1982 : 186.

AUTHORITY. Under Article 36 of the International Code of Nomenclature (coordinate categories), the authority and date of a name in the family group can originate from its use as a subfamily name, so the citation of Verrill, 1899 as author and date for Luidiidae (e.g. by Spencer & Wright in the 'Treatise on Invertebrate Paleontology', 1966) is incorrect.

ORDINAL POSITION. In 1963 Fell, followed by Spencer & Wright (1966) split off the Luidiidae to the order Platyasterida (otherwise including only the lower Palaeozoic family Palasteriscidae) from its longstanding position close to the Astropectinidae because of its transversely matching longitudinal series of adambulacral, actinal and inferomarginal plates. This has never seemed to me satisfactory in view of the close resemblance of *Luidia* and *Astropecten*, especially in transverse section of the arms, and I fully agree with Jangoux (1975) and McKnight (1977), who dismissed Fell's disposition because of close anatomical resemblances between *Luidia* and certain astropectinids, and the different alignment of the ambulacral and adambulacral plates (the Platasteriscidae having only a very shallow ambulacral groove, unlike any recent asteroids). The Luidiidae should therefore be included in the order Paxillosida Perrier, 1884, formerly lumped with Perrier's Valvatida in Sladen's larger order Phanerozonia (1889). Blake (1982) has independently reached the same conclusion on the basis of his more detailed morphological studies of the various series of ossicles, coupled with the absence of any fossil luidiids in pre-Miocene strata. The Luidiidae shares with the Astropectinidae not only the paxilliform abactinal plates but also the presence of superambulacral plates, the knobbed tube feet with double ampullae and the horizontal framework to the body of enlarged marginal plates (though this is not exclusive to the Paxillosida). The main differences are the lack of transverse matching of the actinal series with the adambulacrals and inferomarginals in astropectinids—a character probably not of more than familial weight—and the reduction and paxilliform nature in luidiids of the superomarginals, so that only their position matching the inferomarginals indicates their true identity. (In the Clathrata and Alternata groups of species of *Luidia*, the two lateralmost series of abactinal paxillae each side also match the marginals in length and are indistinguishable from the superomarginal paxillae unless the latter are broadened—which reaches an extreme development in *Luidia (Platasterias) latiradiata* (Gray), referred to the Clathrata group by Blake (1973); other groups of *Luidia* species have smaller lateral abactinal paxillae.)

DIAGNOSIS. A family of Paxillosida with 5–11 fairly long, gently tapering arms (usually described as 'strap-shaped'), not broadening basally into the disc; lower surface almost flat (and in preserved specimens often also the upper, owing to collapse of the fine paxillar reticulum); median paxillae irregular and smaller than the lateral ones, of which at least the two outermost series are arranged in longitudinal series and matched transversely; papulae distributed all over the upper side between the abactinal plates, compound at their outer ends; superomarginal plates paxilliform, similar in structure to the adjacent abactinal plates, though up to twice as long in species where the abactinal paxillae are particularly small (only in the subgenus *Platasterias* of *Luidia* are the superomarginals considerably broader than the lateral paxillae, though still essentially paxilliform); inferomarginal plates massive, lateral or lateroventral in position but never conspicuous in dorsal view, each raised into a flat-topped keel bearing some large spines, especially near the upper end (the ambitus or broadest part of the arm), interspersed with spinelets of varying size, the sides of the keel armed with many fine geometrically-arranged fasciolar spinules; a small actinal plate (rarely two proximally) intercalated between each inferomarginal and the matching adambulacral plate, often acting as the base for a spiniform pedicellaria (in a few species of the Alternata group of *Luidia* there are supernumerary reduced, pedicellaria-bearing actinal plates superimposed on the abradial ends of the adambulacral plates); interradial areas compact, rarely with more than a few series of actinal plates; adambulacral plates broad and raised into a shallow keel, bearing 2–4 large spines along the crest (the fourth, if present, proximal to the third), the innermost (furrow spine) compressed, curved and sabrelike; pedicellariae well developed, sessile, with 2-, 3- or even 4-valves, absent in a few species or individuals, those of the upper side usually nutcracker-like with broad blunt jaws, the marginal and ventral ones more elongated and spiniform; internally, superambulacral plates linking the ambulacrals and inferomarginals; tube feet pointed or ending in knobs, their internal ampullae double.

REMARKS. Döderlein (1920) monographed *Luidia* Forbes, 1839, distinguishing the following groups and subgenera:
Clathrata group: subgenera *Senegaster* and *Petalaster* Gray, 1840;
Alternata group: subgenera *Maculaster, Alternaster* and *Armaster*;
Quinaria group: subgenera *Integraster, Denudaster, Penangaster* and *Quinaster*;
Ciliaris group: subgenus *Hemicnemis* Müller & Troschel, 1840 (other names being Döderlein's).
Fell (1963) pointed out that the type species of both *Luidia* and *Hemicnemis* is *L. ciliaris* (Philippi) so that *Hemicnemis* is a synonym. Except for *Armaster*, which he lumped with

Alternaster, he perfunctorily raised all the others to generic rank, a move which has failed to gain acceptance, notably from Blake (1973) in an exhaustive study of the ossicles of luidiids and related asteroids. At the same time, Blake reduced *Platasterias* Gray, 1871 to the rank of a subgenus of *Luidia* (whereas Fell had included it in the subclass Somasteroidea), since *P. latiradiata* is undeniably more closely related to *Luidia clathrata* (Say) than *clathrata* is to *L. ciliaris*. The family is accordingly considered to be monogeneric.

Where Atlantic taxa of *Luidia* are concerned, the limits between Döderlein's main groups are particularly blurred. For instance, *L. scotti* Bell, 1917 (omitted by Döderlein), now treated as a subspecies of *L. ludwigi* Fisher which Döderlein put under the Alternata group, loses its bold colour pattern characteristic of that group soon after preservation and must have a different pigment to *L. alternata*. Since *L. ludwigi scotti*, together with *L. armata*, also lacks the enlarged abactinal spines found in the majority of species of the Alternata group, it bridges the gap to the similarly smooth species of the Clathrata group, both groups having the two outermost series of abactinal plates matching up with the marginal plates. *L. barbadensis* Perrier has the lateral paxillae only slightly outnumbering the marginals by *c.* 12/10, which serves to differentiate it from the two above groups as defined by Döderlein, who listed it as 'incertae sedis' under the Alternata group. Its coarse and squarish lateral paxillae certainly link it more closely with the Alternata group than with the Quinaria and Ciliaris groups with their finer and more numerous paxillae.

One of the main characters by which at least the Atlantic species of *Luidia* can be split up is the alignment of the inferomarginal plates, whether or not they extend above the ambitus. In the Clathrata and Alternata groups they are ventro-lateral (see Fig. 1a, b) but in the Quinaria and Ciliaris groups they extend higher. The difference in alignment is accompanied by some difference in armament. With more ventrally-aligned inferomarginals, the largest spines are at the ambitus and project horizontally, or nearly so (though if there is more than one ambital spine then the uppermost is more or less reduced); the spines below the ambitus are appreciably smaller also and are somewhat appressed. When the inferomarginals extend on to the upper surface all their spines are erect, the uppermost one (or two) being largest, the top one projecting almost vertically upwards in its natural position, at least on those (often alternate) plates where it arises from its highest locus.

Secondly, the number of lateral paxillae corresponding to the superomarginal ones—whether matching exactly or in excess—is another easily determined character, again dividing the Clathrata and Alternata groups from the Quinaria and Ciliaris ones, though *L. barbadensis* is an exceptional intermediate, as already mentioned.

These two characters are therefore the most important in the tabular key (table 1) to the Atlantic species, besides the obvious difference in arm number for some species. The occurrence of pedicellariae is variable and not reliable for more than local differences at the infraspecific level, though their location and the number of valves may be useful.

ONTOGENY. The reproduction and larval stages of *Luidia sarsi* were studied by Tattersall & Shepherd (1934). An early post-metamorphosal stage of this species is exemplified by the diminutive holotype, R 8 mm, of *Astrella simplex* Perrier, 1882, synonymized with *L. sarsi* by Ludwig (1897).

Fully metamorphosed specimens of other species taken by the *Pillsbury* in the tropical Atlantic show that all the primary plates, even the small actinal ones, occur from an early stage, though the actinals at first lack any armament.

At R *c.* 6 mm, the upperside paxillae of each arm consist of a band of somewhat irregular median paxillae flanked on either side by two complete regular longitudinal series, the outer of which is the superomarginal series and the other the primary lateral series. Almost immediately a secondary lateral series begins to develop proximally between the two but probably does not become fully developed to the arm tip until R is *c.* 25 mm, at least in *L. alternata numidica* Koehler. In *L. heterozona* Fisher, where the lateral paxillae are relatively smaller, the secondary lateral series is not initiated until R *c.* 25 mm and is still not quite complete at R 50 mm. At least in species with fairly coarse paxillae, the primary lateral

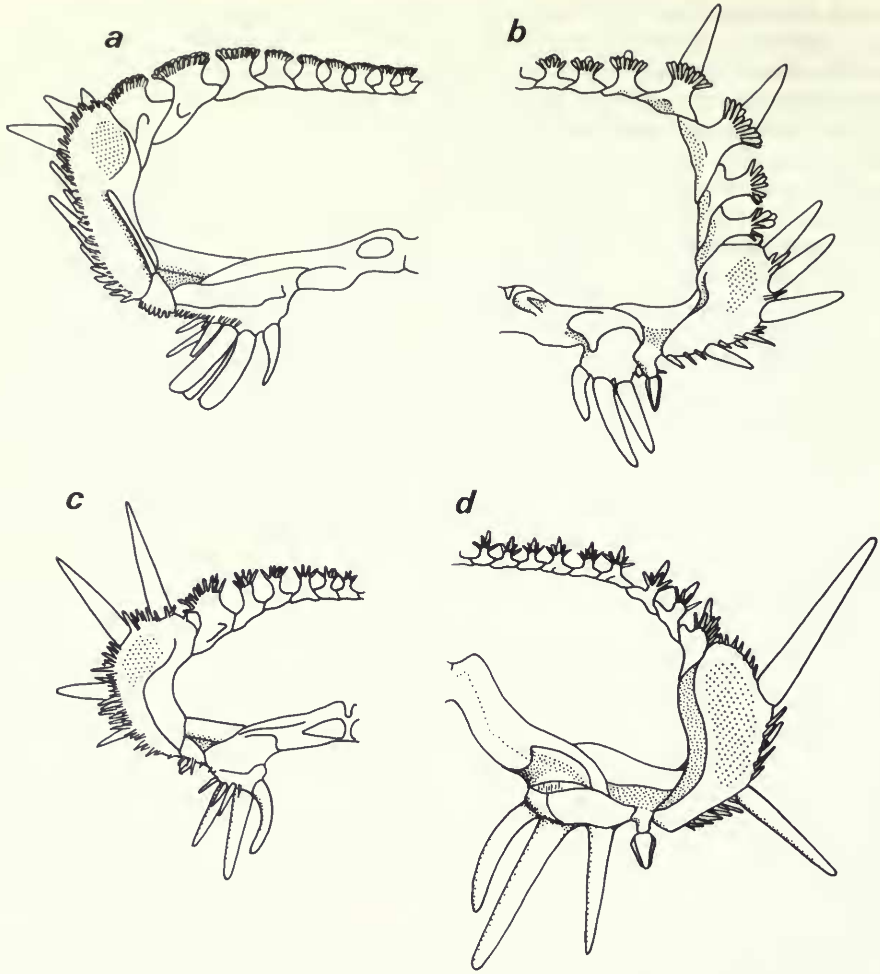

Fig. 1 Half arm sections, viewed from the proximal side, of: (a) *Luidia clathrata, Pillsbury* st. 652, R *c.* 120 mm; (b) *L. alternata alternata, Pillsbury* st. 767, R *c.* 90 mm; (c) *L. sarsi elegans. Albatross* st. 2177, R *c.* 115 mm; (d) *L. sagamina aciculata, Atlantide* st. 61, R *c.* 90 mm.

series can usually be recognised by the fact that both its abradial and adradial basal lobes are overlain by the opposing lobes of the secondary lateral and outermost median series of paxillae respectively (see Fig. 1a, b, d) but this does not always hold good when the skeleton is more delicate. The median paxillae also increase in number to some extent, less so in species where they are stouter, as in *L. alternata* (Say) where the total number of paxillae across the arm proximally between the two opposite superomarginal series increases from 9 or 10 at R 6 mm to only *c.* 12 or 13 at R 50 mm. There are still only *c.* 12 in the largest specimen of *L. alternata alternata* studied, R 175 mm, so the tabula of the larger paxillae in such species may be markedly broadened.

With regard to the armament, as usual in newly metamorphosed asteroids, the spinelets and future spines are all attenuated, often trifid, with the terminal point prolonged. This is still true up to R *c.* 9 mm, except for the furrow and second adambulacral spines, which are simple and unbranched, though still uniform in length with the other spinelets. At R *c.* 10 mm, an ambital inferomarginal spine begins to enlarge in *L. alternata* and the second adambulacral spine also increases disproportionately in size, while a few of the more lateral paxillae begin to develop a single large central spine. In species with a third adambulacral

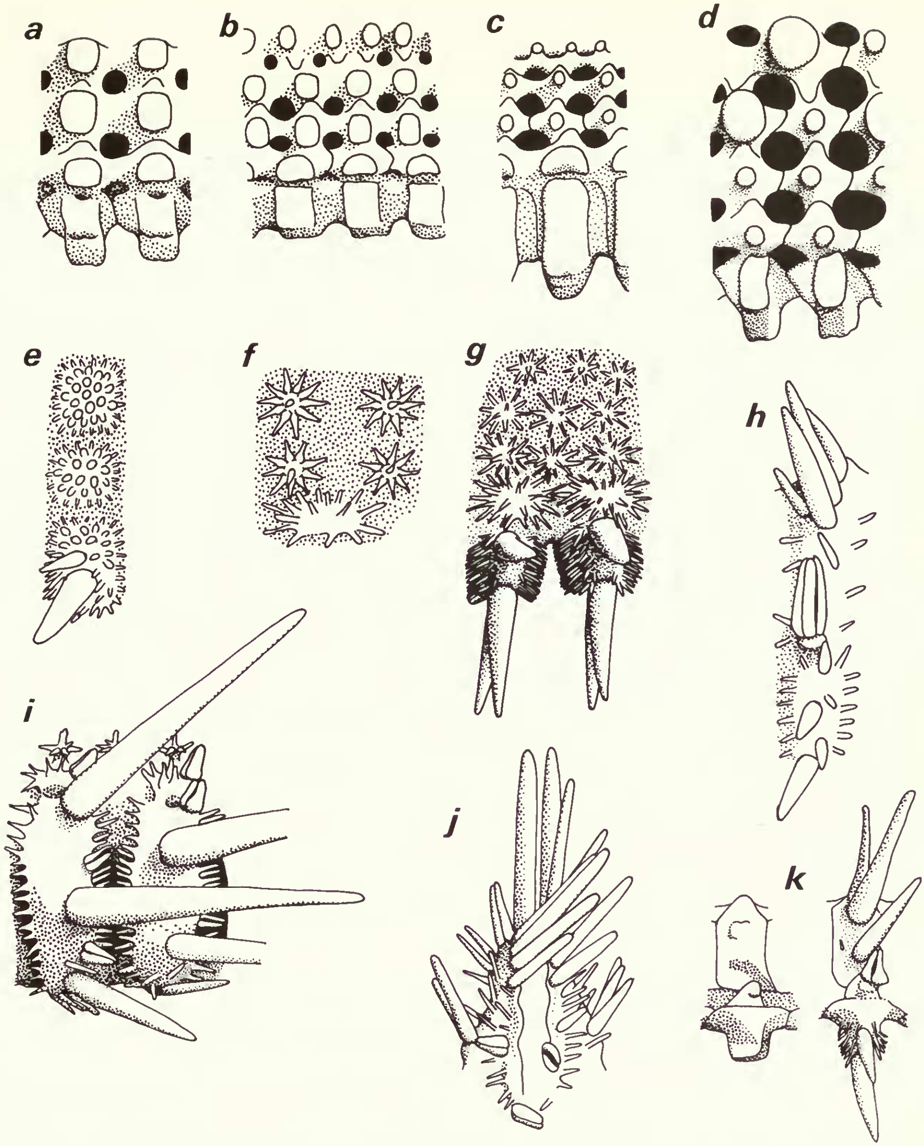

Fig. 2 (a to d) Dorsal views of a proximal part of an arm, showing the upper ends of several inferomarginals, the adjacent superomarginals and some abactinal plates, denuded: (a) *Luidia ludwigi scotti*, paratype, *Terra Nova* st. 42, R 62 mm; (b) *L. barbadensis, Gerda* st. 239, R *c.* 130 mm; (c) *L. sarsi elegans* (as in Fig. 1c); (d) *L. alternata alternata, Pillsbury* st. 767, R *c.* 75 mm; (e to g) the same views with armament entire (inferomarginal omitted in (f)) of: (e) *L. ludwigi scotti* (as in Fig. 2a); (f) *L. heterozona barimae, Pillsbury* st. 652, R 200+ mm; (g) *L. sarsi africana,* Namibia, R *c.* 100 mm; (h) one adambulacral, actinal and inferomarginal, in ventral view of *L. alternata alternata* (as in Fig. 1b); (i) *L. heterozona heterozona, Pillsbury* st. 24, R 100+ mm, lateral view of two successive inferomarginals and superomarginals with a few lateral paxillae; (j) apex of jaw of *L. heterozona barimae* (as in Fig. 2f); (k) *L. sagamina aciculata*, (as in Fig. 1d), two lines of adambulacral, actinal and inferomarginal plates, the one on the left denuded. The proximal side is to the right in (a–g), to the left in (h, i & k).

Table 1 Tabular key to the Atlantic species of *Luidia*. Entries in brackets signify occasional occurrence.

	1	2	3	4	5	6	7	8	9	10	11
senegalensis	9(8)	–	10	c	–	vl	–	2	4	–	–
clathrata	5	–	10	c	–	vl	–	2(3)	4	–	–
ludwigi scotti	5	+	10	c(s)	–	vl	–	2(1)	4	3	–
patriae	5	–?	10	u	–	vl	–	2	4	–	–
alternata (2 subspp.)	5	+	10	S	–	vl	–	2,3	3($\frac{1}{2}$)	3	–
barbadensis	6	–	12–13	c	–	vl	–	3(2)	4	3	–
sagamina aciculata	5	–	16–19	s	+	l	+	2/3	2(3)	3	+
heterozona (2 subspp.)	10	–	15–18	u	+	l	+	3/2,4/3	(4)3	2	+
sarsi (3 subspp.)	5	–	17–20	u	+	l	+/–	4/3,3/2	3($\frac{1}{2}$)	2	+(–)
atlantidea	5	–	15–19	c	–	l	+/–	3/2(4)	3($\frac{1}{2}$)	2	+(–)
ciliaris	7(8)	–	15–18	c	(+)	l	+	3–5	2	–/3	–

1. Arm number.
2. Colour pattern of upper side:
   + — patchy (may fade in long-preserved *L. ludwigi scotti*).
   – — uniform or darker along midradial area or lighter along midradial area or lighter along superomarginal or adjoining lateral paxillae.
3. Number of consecutive lateral paxillae corresponding to 10 superomarginal ones.
4. Paxillar armament:
   c — central spinelets distinctly coarser than peripheral ones.
   u — central and peripheral spinelets uniform.
   s — one central spinelet both longer and stouter on most paxillae.
   S — one central spine (1–5 mm long) abruptly enlarged on some scattered (mostly lateral) paxillae.
5. Shape of superomarginal paxillae:
   + — elongate.
   – — rounded or squarish.
6. Alignment of inferomarginal plates:
   l — lateral.
   vl — ventro-lateral.
7. Inferomarginal spines:
   + — alternating on consecutive plates.
   – — all on the same levels.
8. Number of large erect inferomarginal spines.
9. Number of adambulacral spines.
10. Number of valves on actinal pedicellariae (when present, – = absent).
11. Oral furrow pedicellariae:
    + — present.
    – — absent.

spine in the adult, this is probably evident proximally by R 12–15 mm and the other spines and spinelets grow and coarsen into their adult proportions at this size or soon after. *Luidia sagamina aciculata* Mortensen is exceptional in the development of the third adambulacral spine, which may be lacking altogether, especially in american specimens, judging from the few so far studied. Increase in numbers of spines also shows a growth gradient along the arm. In *L. heterozona* Fisher, for instance, only about four proximal adambulacral plates have the third spine enlarged at R 20 mm but there is even a fourth spine on the first 10–15 plates, and almost equal to the fully developed third one, by R *c*. 80 mm.

Actinal and abactinal pedicellariae, when developed, probably first appear between R 15 and 20 mm but oral furrow pedicellariae, for example in *L. heterozona*, are not fully modified from pairs of spines until R exceeds *c*. 50 mm.

Previous works. Useful relevant publications on the Luidiidae include the general monograph of Döderlein (1920), Nataf & Cherbonnier (1973) on the tropical West African area and Downey (1973) and Walenkamp (1976 and 1979) on the West Indian area.

Distribution. The species of *Luidia* are mostly restricted to the shelf, though several Atlantic taxa extend to the upper bathyal, including *L. barbadensis* to 430 metres, *L. ciliaris* to 400 metres, *L. heterozona* and *L. sagamina aciculata* to 975 metres and *L. sarsi* exceptionally to 1300 metres. (The maximum depth for both *L. heterozona* and *L. sagamina aciculata* derives from *Jean Charcot* (Walda cruise) st. 40, *c.* 04° 07′ N, 01° 35′ W, off Ghana, 975 metres, and is surprising since previous maxima for the two respectively were only 400 and 150 metres, cited by Nataf & Cherbonnier (1973), the vast majority of records for both species being from 50–100 metres.)

Geographically, five Atlantic taxa appear to be restricted to the american side of the ocean, namely *L. barbadensis, L. clathrata, L. ludwigi scotti, L. patriae* and *L. senegalensis* (the last despite its name), while *L. atlantidea* and *L. ciliaris* are entirely eastern (american records for *L. atlantidea* proving incorrect, see p. 168. The remainder are distributed as follows:

West Atlantic	East Atlantic
alternata—N Carolina to N Argentina	*numidica*—Senegal to Zaire (Congo)
barimae—Venezuela to French Guiana	*heterozona*—Mauritania to Angola
sagamina aciculata(?)—N Carolina to Florida Strait	*sagamina aciculata*—Mauritania to Zaire & St Helena
elegans—E U.S.A. & Gulf of Mexico	*sarsi*—Norway to Mauritania & Azores
elegans(?)—S Brazil	*africana*—SW & S of southern Africa

The relationships of these are discussed below to assess their respective ranks.

LUIDIA Forbes

Luidia Forbes, 1839 : 123; Sladen, 1889 : 244–248; Fisher, 1911 : 105; Süssbach & Breckner, 1911 : 198; Döderlein, 1920 : 193–246; Bernasconi, 1943 : 3–5; A. M. Clark, 1953 : 379–380; Fell, 1963 : 433; Downey, 1973 : 21–22; Tommasi, 1974 : 7; A. M. Clark & Courtman-Stock, 1976 : 43. Type species: *Luidia fragilissima* Forbes, 1839 (a synonym of *Asterias ciliaris* Philippi, 1837), by monotypy.

Hemicnemis Müller & Troschel, 1840 : 105; Döderlein, 1920 : 217 (as subgenus). Type species: *Asterias ciliaris* Philippi, 1837.

Petalaster Gray, 1840 : 183: Döderlein, 1920 : 215 (as subgenus). Type species: *P. hardwicki* Gray, 1840, cited by Fisher, 1911 (though with *Petalaster* in synonymy), non *P. columbia* Gray, designated by Fell, 1963.

Luydia (lapsus) Düben & Koren, 1846 : 254.

Astrella Perrier *in* Milne-Edwards, 1882 : 21. Type species: *A. simplex* Perrier, 1882 (a synonym of *Luidia sarsi* Düben & Koren, 1845), by monotypy.

Senegaster, Maculaster, Alternaster, Armaster, Integraster, Denudaster, Penangaster & Quinaster (subgenera) Döderlein, 1920 : 215–217, raised to generic rank by Fell, 433–434 (except for *Armaster*).

Luidia alternata (Say)

Figs 1b, 2d, h, 3a–i, 4, 5

Asterias alternata Say, 1825 : 144–145.

Luidia alternata: Lütken, 1859 : 42–43; Perrier, 1875 : 334–336 [1876 : 254–256]; Sladen, 1889 : 250–251, 740; Verrill, 1915 : 201–203 [non *L. alternata bicolor*]; Döderlein, 1920 : 241, 267–268, figs 7, 11; H. L. Clark, 1933 : 20, pl. 1; Bernasconi, 1943 : 14–15, pl. 3, figs 1, 6, pl. 4, fig. 1; Engel & Schroevers, 1960 : 6; Ummels, 1963 : 97–98, pls 8, 10; Gray, Downey & Cerame-Vivas, 1968 : 138, fig. 6; Tommasi, 1970 : 8, pl. 8, fig. 24; Downey, 1973 : 23–24, pl. 2, figs A, B; Blake, 1973 : 33–34, pl. 6, figs 25–42; Walenkamp, 1976 : 29–32, figs 6, 7, pl. 3, fig. 3, pl. 4, fig. 4.

Luidia granulosa Perrier, 1869 : 109–110, pl. 2, fig. 18.

Luidia variegata Perrier, 1875 : 337 [1876 : 257].

Luidia numidica Koehler, 1911 : 3, pl. 1, figs 8–11; 1914 : 167, pl. 4, fig. 7; Döderlein, 1920 : 235, 242; Nataf & Cherbonnier, 1973 : 71–74, pl. 1, figs A, C, pl. 5, figs 1, 2, pl. 7, fig. 6, pl. 9, figs A–D.

Luidia quequenensis Bernasconi, 1942 : 253; 1943 : 15–18, pl. 2, fig. 4, pl. 3, figs 2, 3, 7, pl. 5, figs 1, 2; 1960 : 21–22, pl. 3, fig. 1; Carrera-Rodriguez & Tommasi, 1977 : 65.

Luidia bernasconiae A. H. Clark, 1945 : 19–21; Gray, Downey & Cerame-Vivas, 1968 [?pt] : 138, fig. 7; Downey, 1973 : 25.

Luidia alternata var. *numidica*: Madsen, 1950 : 206–209, fig. 9.

Luidia alternata numidica: A. M. Clark, 1953 : 388–389, pl. 41, fig. 1; 1955 : 22; Engel & Croes, 1960 : 11–12, pl. 6, figs. 1, 2.

R up to 175 mm. R/r ranging from *c.* 5–6/1 at R 30–40 mm to 7–9/1 at R > 70 mm.

A species of *Luidia* with normally 5 arms; abactinal paxillae with about 4 longitudinal series each side also forming transverse rows with the matching but distinctly smaller superomarginal paxillae, though irregularities may occur where the paxillae of the second and third (sometimes other series) are markedly enlarged and bear a single stout central spine fringed by usually several rings of spinelets, the large spines similar in magnitude to the ambital inferomarginal spines, rarely some of the lateralmost series and many of the median paxillae may have a smaller central spine developed; inferomarginal plates primarily ventral in position, only narrowly visible dorsally, armed at the ambitus with 2 or 3 large spines, usually projecting approximately horizontally, and on the ventral side with 2–4 smaller and somewhat flattened spines among the spinelets: adambulacral plates with 3 large spines in a row at right angles to the furrow, sometimes a more or less enlarged spine proximal to the lateralmost one; elongate, 3- or 4-valved pedicellariae, present on some proximal actinal plates (rarely also on the outer ends of the first few adambulacral plates) the slender valves usually only meeting at the tips; shorter, more often bivalved pedicellariae sometimes present (especially in west african specimens) on some abactinal and/or superomarginal paxillae, no pedicellariae on the furrow face of the oral plates. Colour boldly patterned on the upper side with a dark pentagon on the disc and three to five transverse dark bands, brown, black, greenish or purple, on each arm, the remainder being yellow, cream or white.

STATUS OF *L. numidica.* Madsen (1950) treated *Luidia numidica* Koehler as a west african variety of *L. alternata* and noted that the only difference appeared to be the smaller number of spine-bearing paxillae in *numidica.* A. M. Clark (1953) used subspecific rank for *numidica* but noted that a specimen from the Cape Verde Islands with relatively numerous spino-paxillae is very similar to some west Atlantic specimens of *L. alternata*. In 1973, Nataf & Cherbonnier treated *numidica* as a full species but without comparisons or any comment on its status.

Koehler (1911) had only two specimens from West Africa, a poor dry one with R 52 mm and the broken holotype, r 13 mm so R probably 80–100 mm. He remarked on the closeness to *L. alternata* but distinguished that species by the more numerous inferomarginal and paxillar spines, the more attenuated pedicellariae and the 'quite different' paxillae with the peripheral spinelets thin and elongated, not short, thick and granuliform. Study of *c.* 30 and 15 specimens from west and east Atlantic respectively, mostly from the *Gerda* and *Pillsbury* collections, now indicates that, although the armament of the paxillae is somewhat variable in both east and west Atlantic specimens and is also subject to some extent to growth changes, there is a consistent difference in the armament of the smaller paxillae if total size is taken into account and also a significant difference in the number (often also the shape) of the large paxillar spines. Already in west african specimens at R 20–25 mm, over half the median paxillae have more than one (usually 2–4) short coarse similar central spinelets; at R 40–50 mm these number 3–6 and at R *c.* 60 mm usually 4–8 (see Fig. 3h, i). In *L. alternata* from the western Atlantic, even at R 100 mm or more, many central paxillae still only have a single more or less coarser central spinelet, the maximum number being about 4. However, these large specimens may have some median paxillae with the peripheral spinelets arranged in two concentric rings of 6–10 each, the outer ones being more slender and cylindrical than the inner ring, the spinelets of which are transitional in shape to the central spinelet (or spine). In general, the shape of the peripheral spinelets can usually be called subclavate but

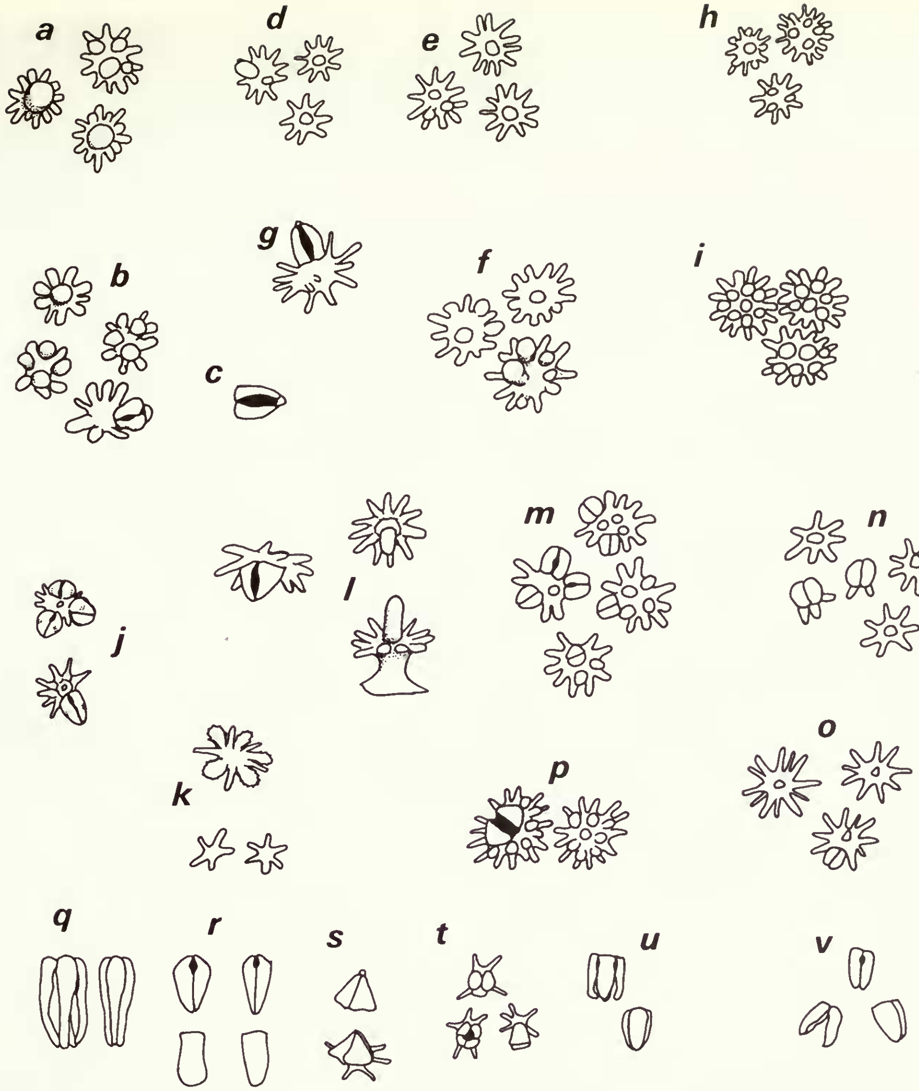

Fig. 3 (a, b, d–p) Abactinal paxillae, (c, q–v) pedicellariae. (a–g) *Luidia alternata alternata*, (a) type material of *L. quequenensis*, Quequen, N Argentina, R 72 mm, median paxillae; (b) holotype of *L. bernasconiae*, R 100 mm; (c) the same, superomarginal pedicellaria; (d) *Gerda* st. 1038, R 40 mm, median paxillae; (e) *Oregon* st. 4215, R *c.* 60 mm, median paxillae; (f) *Pillsbury* st. 654, R 100+ mm; (g) *Pillsbury* st. 767, R *c.* 90 mm, superomarginal paxilla; (h, i) *L. alternata numidica*: (h) *Pillsbury* st. 248, R only *c.* 22 mm; (i) Cape Verde Is, R 55–60 mm; (j) *L. heterozona heterozona, Pillsbury* st. 68, R *c.* 100 mm, disc paxillae; (k) *L. ciliaris*, Naples, R 140 mm, inner lateral paxilla (above) and two median paxillae; (l) *L. sagamina aciculata, Atlantide* st. 61, R *c.* 90 mm, superomarginal paxilla (left) and lateral paxillae from above and the side (below); (m) *L. sarsi sarsi*, W. of Scotland, R *c.* 100 mm, median paxillae; (n) *L. sarsi sarsi*, paratype of *L. africana, Porcupine* st. 36, R *c.* 85 mm, disc paxillae; (o) *L. sarsi elegans, Gerda* st 456, R *c.* 60 mm, median paxillae; (p) *L. atlantidea, Pillsbury* st. 26, R *c.* 100 mm, lateral paxillae; (q) *L. alternata alternata, Oregon* st. 4190, actinal pedicellariae; (r) *L. heterozona heterozona, Pillsbury* st. 259 (left) and 49 (right), actinal pedicellariae in two views; (s) *L. sagamina aciculata, Atlantide* st. 61, two actinal plates, one armed only by the pedicellaria, pedicellariae slightly foreshortened; (t) *L. ludwigi scotti*, paratype, actinal paxillae with 2-, 3- and 4-valved pedicellariae, foreshortened; (u) *L. ludwigi scotti, Pillsbury* sts 1384 & 842, lateral views of 4- and 3-valved actinal pedicellariae; (v) *L. sarsi sarsi*, Shetland Is, lateral views of actinal pedicellariae.

alternate ones may be hardly at all expanded at the tips on the slightly larger paxillae. As for the large paxillar spines on the second and third lateral series of paxillae particularly, even in the Cape Verde Islands specimen mentioned in 1953 only *c.* 35%, at most, of these lateral paxillae have the large spines. In other specimens from West Africa the percentage is usually *c.* 20. The shape of the spines is also relatively squat, their length most often 1–2 mm, the longest (in Koehler's large holotype) 3 mm, the length/basal breadth usually less than 3/1. In american specimens such squat spines may also occur but usually the length/breadth ratio is 4·0–4·5/1 and the length may exceed 3 mm even at R only 60 mm.

The conclusion reached from these observations is that the specimens from the two sides of the Atlantic are conspecific but the west african form can be recognized as a distinct subspecies *numidica* of *L. alternata*, distinguished by the more 'plushy' superficial appearance of the abactinal paxillae, interspersed with shorter and fewer large spines.

Synonymy. *Luidia granulosa* Perrier, 1869 was recognized as a synonym of *L. alternata* by Perrier himself in 1875 and *L. variegata* Perrier, 1875 by Verrill, 1915. In 1950, Madsen (cited by A. M. C., 1953 : 380) also referred *L. bernasconiae* A. H. Clark, 1945, to the synonymy but this was refuted by Downey in 1968 & 1973, who maintained that it has only two adambulacral spines, not three or four, and the non-spine-bearing paxillae have 5–10 clavate peripheral spinelets compared with 10–16 slender acute ones in *alternata*, though on p. 23 of the 1973 paper she describes the peripheral paxillar armament of *alternata* as subclavate. The dried holotype of *L. bernasconiae* certainly shows swollen-tipped peripheral paxillar spinelets more clavate than usual for *L. alternata* but it regularly has three large and a fourth smaller adambulacral spine, as described by A. H. Clark, the common number for *L. alternata*. In view of the variability in shape of the paxillar armament in *L. alternata* already mentioned, it is difficult to maintain *bernasconiae* as distinct. If there are specimens from North Carolina as described by Gray, Downey & Cerame-Vivas (1968) with sporadic large spines but only two adambulacral spines, then these may have to be nomenclatorially distinguished but not as *L. bernasconiae*. The superficial difference in proportions between *L. alternata* and *L. bernasconiae* suggested by the photographs in the 1968 paper is correlated with the much larger size (R *c.* 135 mm, judging from the scale) of the specimen named *alternata*, and exaggerated by the greater reduction so that both appear of similar size though R is only *c.* 77 mm in the specimen named *L. bernasconiae*.

With regard to *Luidia quequenensis* (and other species of *Luidia* described by her) Bernasconi, 1942 confusingly modified the terminology of the lateral abactinal paxillae used by Döderlein (1920, see pl. 18, caption) as follows: his 'Randpaxillen' (i.e. the superomarginal paxillae) become her 'paxilas marginales'; his 'untere Seitenpaxillen' (the two [primary and secondary] outermost series of lateral paxillae) become her 'paxilas inferomarginales'; his 'obere Seitenpaxillen' (the third and fourth series or two outer series of median paxillae) become her 'paxilas superomarginales'. This odd terminology has unfortunately been perpetuated by Carrera-Rodriguez & Tommasi (1977). Bernasconi distinguished *L. quequenensis* from *L. alternata* in 1943 (pp. 5, 17) by the large number and coarse shape of the spines of the 'paxilas superomarginales', which should be the third and fourth series of paxillae from the true superomarginal ones. However, a specimen from Quequen, kindly presented to the British Museum by Dr Bernasconi, shows numerous spinopaxillae but more of these are in the second from outermost lateral series (what I call the primary row), though the third series also has a considerable number. However, there are many inconspicuous spineless paxillae also in these series so that even the second only has *c.* 64% of spinopaxillae out of well over 100 paxillae counted on several arms. The largest number of consecutive spinopaxillae found was only 9. Similar frequencies of over 60% of spinopaxillae in the second or third lateral series may occur throughout the range of *L. alternata alternata*, for instance in some of the *Challenger* specimens from Bahia, NE Brazil, others from French Guiana (*Oregon* and *Pillsbury* collections) and from Georgia (the holotype of *L. bernasconiae*).

Neotype. In the event of future disagreement with the synonymies now proposed and in the

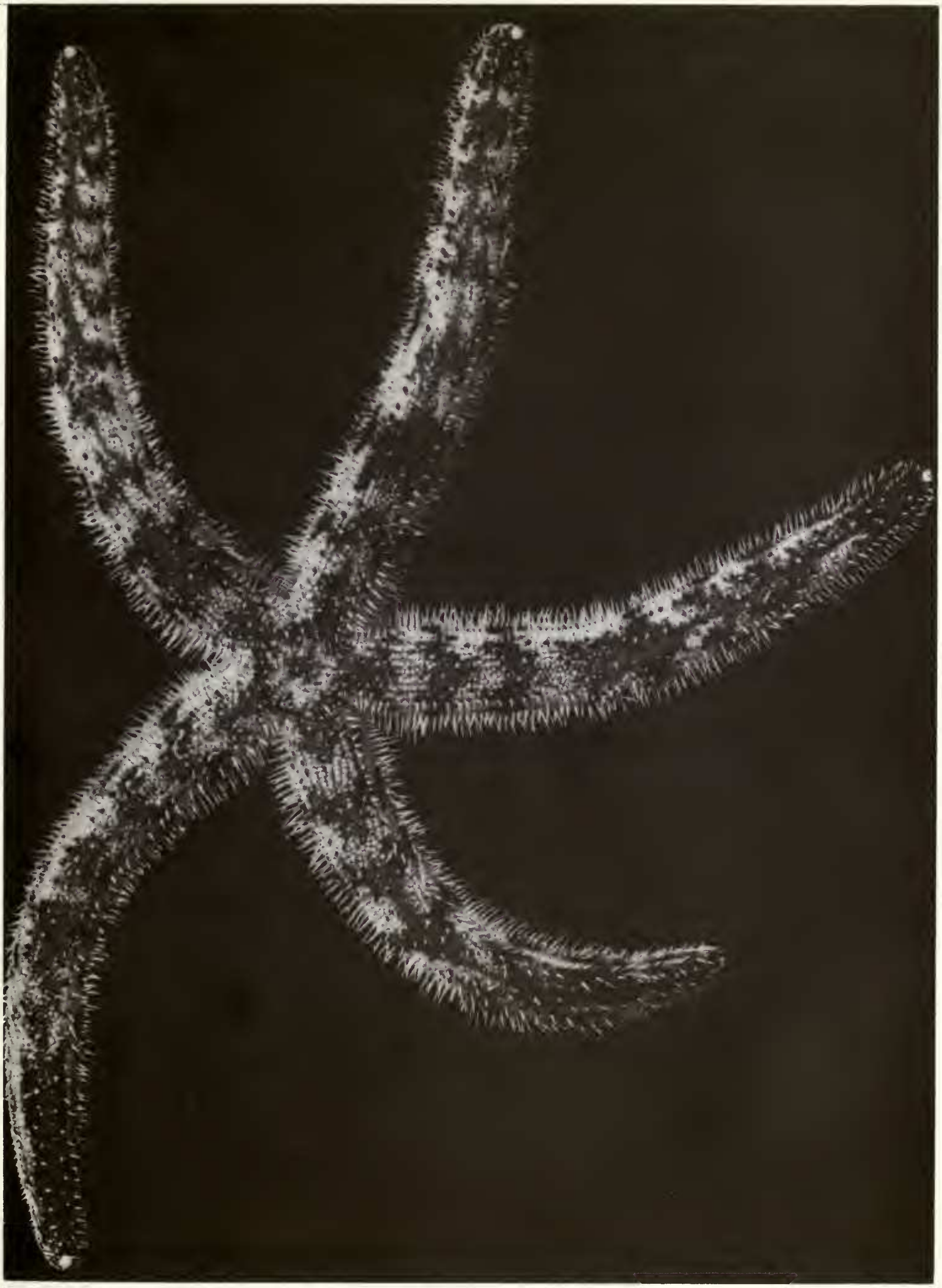

Fig. 4 *Luidia alternata alternata* (Say), neotype, BM(NH) reg. no. 1937.5.9.6, Dry Tortugas. Dorsal view, × 0·6.

absence of Say's type material (apparently long-lost), it is very desirable that a neotype from the vicinity of Florida, the type locality, should be nominated. Accordingly I propose a beautiful specimen from the Dry Tortugas now in the British Museum collections, registered number 1937.5.9.6, collected by Colman and Tandy, shown in Figs 4 and 5.

The arms vary in length so that R ranges from 150–175 mm; r is *c.* 19 mm and R/r = 7·9–9·2/1. Spinopaxillae are fairly numerous on the proximal primary (second) lateral series but become more sporadic distally (*c.* 55% of 100+ primary paxillae from proximal parts of several arms are spine-bearing). The longest spines measure 4·0 mm in length. Progressively fewer of the third, fourth and fifth series of paxillae are also enlarged with spines but none of the first series or the adjoining superomarginal paxillae and very few midradial paxillae. The median paxillae without enlarged spines have at least one central and about 9 peripheral spinelets, the latter almost cylindrical and blunt-tipped but the slightly larger paxillae have up to 4 central and *c.* 20 peripheral spinelets, the latter in a double ring of which the inner ones are subclavate and transitional in shape to the shorter, coarser central spinelets. The inferomarginal plates mostly bear two large ambital spines up to 7 mm long, slightly irregular in position on consecutive plates but not regularly alternating. There are 2–4, usually 3, more irregular smaller spines on the ventral side of each plate. Most of the primary actinal plates bear a long slender 3- or sometimes 4-valved pedicellaria and proximally also one or two additional pedicellariae based on supernumerary platelets superimposed on the lateral ends of the adambulacral plates. Most adambulacral plates have 3 large spines and a smaller fourth one proximal to the third (lateral-most). On the proximal plates this fourth spine may reach a similar length to the others.

DISTRIBUTION. *L. alternata alternata* from North Carolina to northern Argentina (*c.* 38° S); 0–160 metres.

L. alternata numidica from Senegal to Zaire (Congo), West Africa; 10–100 metres.

Luidia atlantidea Madsen
Fig. 3p

Luidia africana: Koehler, 1911 : 19; Döderlein, 1920 : 288–289; Mortensen, 1925 (pt) : 178. [Non *L. africana* Sladen, 1889.]

Luidia atlantidea Madsen, 1950 : 192–198, fig. 5, pl. 16, figs 1, 2; A. M. Clark, 1953 : 393, 394; 1955 : 22, 32; Nataf & Cherbonnier, 1973 : 76–80, pl. 1, fig. B, pl. 2, figs A, B, pl. 7, figs 1–5, pl. 9, figs E, F. [Non *L. atlantidea*: Downey, 1973 : 25 = *L. sagamina aciculata*.]

Luidia sarsi: Studer, 1884 : 43. [Non *L. sarsi* Düben & Koren, 1845.]

DISTRIBUTION. On re-examination, the specimen from North Carolina mentioned under the name of *L. atlantidea* by Downey (1973) proved to be *L. sagamina aciculata*. It has a white band along each side of the paxillar area on the arms but this is situated on the two regular rows of *lateral* paxillae, not on the superomarginal series as in *L. atlantidea*. It has not been possible to check the Halpern record cited by Downey but the likelihood is that this too would have been a similar misidentification.

The species is recorded from Atlantic Morocco to Zaire, including the Cape Verde Islands, 10–80 metres.

Luidia barbadensis Perrier
Fig. 2b

Luidia barbadensis Perrier, 1881 : 29; 1884 : 267 [non pl. 10, figs 7, 8, probabaly = *L. sarsi elegans*]; Verrill, 1915 : 205–207, pl. 24, fig. 1; Döderlein, 1920 : 216; H. L. Clark, 1941 : 25; John & A. M. Clark, 1954 : 145; Cherbonnier, 1959 : 170, fig. 3B, E, fig. 4; Downey, 1973 : 24–25; Carrera-Rodriguez & Tommasi, 1977 : 67–71, figs 5–9.

Luidia convexiuscula Perrier, 1881 : 30; 1884 : 268, pl. 10, fig. 6; Verrill, 1915 : 207.

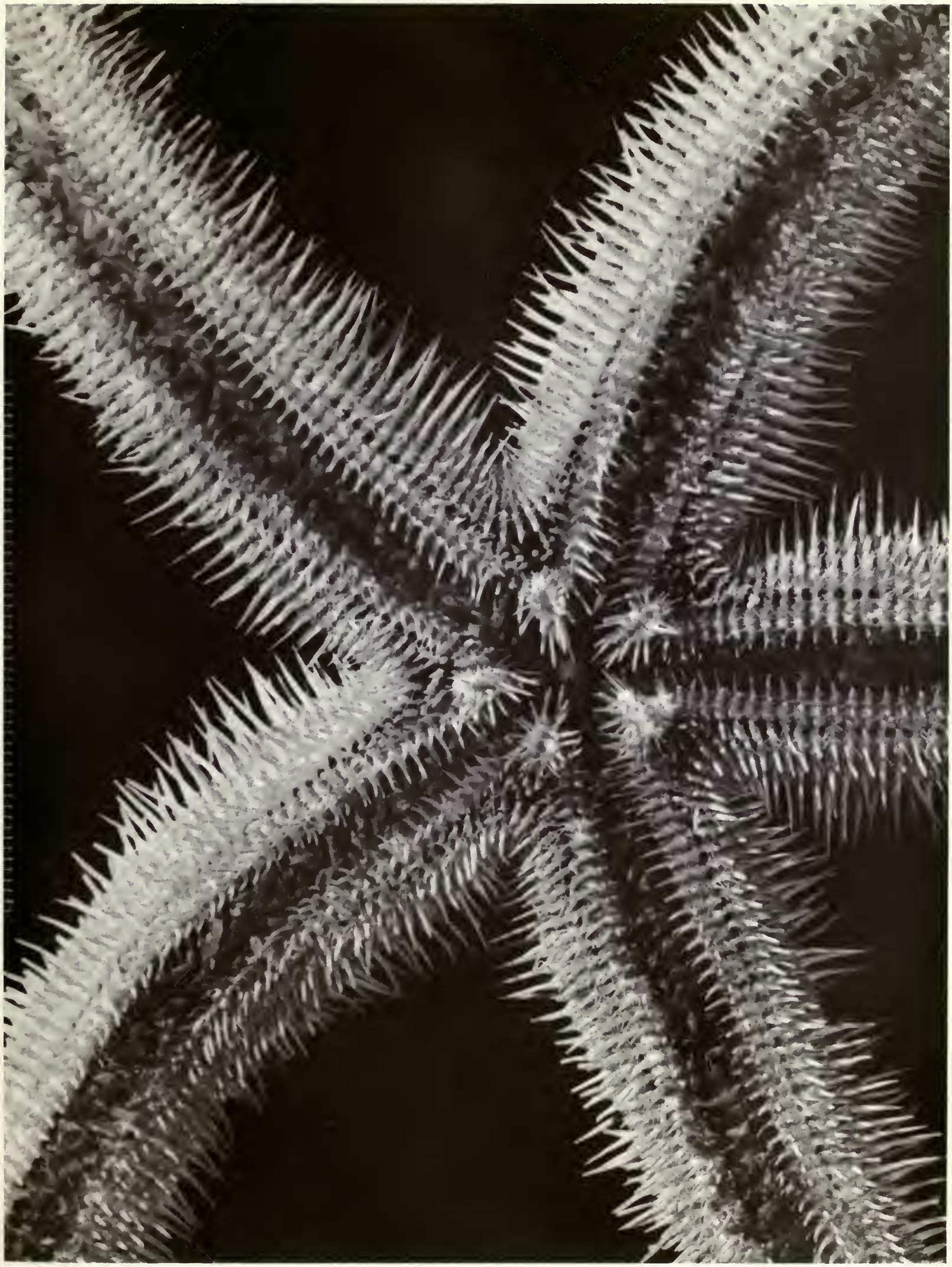

Fig. 5 *Luidia alternata alternata*, neotype. Ventral view of proximal part. × 1·7.

REMARKS. Records of five-armed specimens of *L. barbadensis* are probably based on specimens of *L. sarsi elegans*, which is partially sympatric with it. Certainly the five-armed specimen captioned as *L. barbadensis* by Perrier, 1884, pl. 10, figs 7, 8, appears to be *elegans*, which also differs in the much finer paxillae and the long marginal spines. All 36 *Gerda, Pillsbury* and *Oregon* specimens of *barbadensis* which I have seen have 6 arms.

DISTRIBUTION. Southern Florida and the immediately adjacent Gulf of Mexico, southern Bahamas, to SW Caribbean off Nicaragua and east and south to southern Brazil (*c.* 30° S), 73–430 metres.

Luidia ciliaris (Philippi)
Fig. 3k

Asterias ciliaris Philippi, 1837 : 144.
Luidia fragilissima Forbes, 1839 : 123; 1841 (pt) : 135–140, fig. on p. 135 [7-armed specimens].
Hemicnemis ciliaris: Müller & Troschel, 1840 : 104.
Luidia ciliaris: Perrier, 1875 : 342 [1876 : 262]; Sladen, 1889 : 254; Ludwig, 1897 : 61–85, pl. 4, figs 1, 2, pl. 6, figs 25–36; Süssbach & Breckner, 1911 : 209–210; Döderlein, 1920 : 287, figs 8, 17, 34; Koehler, 1921 : 55, fig. 41; Mortensen, 1927 : 90, fig. 89a; Madsen, 1950 : 205–206, fig. 8; Ursin, 1960 : 30–31; Tortonese, 1965 : 148–150, fig. 68; Blake, 1973 : 40, pl. 10, figs 1–26.

DISTRIBUTION. NE Atlantic, from southern Norway, the Skagerrak, Shetlands, Faeroe Channel, south to the Canary Islands and Azores (?Cape Verde Islands); 1–400 metres.

Luidia clathrata (Say)
Fig. 1a

Asterias clathrata Say, 1825 : 142. [Non *A. clathrata* Pennant, 1777.]
Luidia clathrata: Lütken, 1859 : 37–39; Perrier, 1875 : 332–333 [1876 : 252]; Sladen, 1889 : 253; Verrill, 1915 : 200–201, pl. 24, fig. 2; Döderlein, 1920 : 238, 239, 251–252, figs 1, 21; H. L. Clark, 1933 : 19–20; Bernasconi, 1943 : 6–7, pl. 2, fig. 1; A. H. Clark, 1954 : 375; Ummels, 1963 : 95–97, pls 10, 11; Gray, Downey & Cerame-Vivas, 1968 : 139, fig. 8; Downey, 1973 : 22–23, pl. 1, figs C, D; Blake, 1973 : 30–31, pl. 3, figs 1–28; Walenkamp, 1976 : 19–25, figs 2–4, 19a, pl. 3, fig. 2; 1979 : 11–12.

NOMENCLATURE. Although A. H. Clark (1954) pointed out that *Asterias clathrata* Say was preoccupied by Pennant's earlier senior homonym, he commented that 'nothing would be gained by displacing this well established name' and so continued to use it for this common West Indian species. Unfortunately, under the rules of nomenclature (Article 59(a)) such a junior primary homonym 'must be permanently rejected', that is unless the International Commission can be prevailed upon to use its plenary powers to suppress the earlier name (itself a synonym of *Asterias rubens* Linnaeus, 1758), which action is being requested in a separate proposal.

DISTRIBUTION. North Carolina (??New Jersey), Bermuda and the Gulf of Mexico to southern Brazil (*c.* 31° S); 0–175 metres but rarely below 70 metres.

Luidia heterozona Fisher
Figs 2f, i, j, 3j, r

Luidia heterozona Fisher, 1940 : 265–268, fig. M4, pl. 23; Madsen, 1950 : 203–205; John & A. M. Clark, 1954 : 148; A. M. Clark, 1955 : 33; Cherbonnier, 1963 : 182; Nataf & Cherbonnier, 1973 : 74–76, pl. 4, figs A, B, pl. 5, figs 3–6, pl. 9, figs I, J; Sibuet, 1975 : 284, 288.
Luidia mortenseni Cadenat, 1941 : 53–67, figs 1–3; Cherbonnier, 1963 : 182.
Luidia barimae John & A. M. Clark, 1954 : 145–148, figs 3, 4, pl. 6, fig. 2; Downey, 1973 : 25; Walenkamp, 1976 : 18–19, pl. 1, figs 1–3.

R up to 255 mm; R/r 7–11/1. Of over 150 specimens from both sides of the Atlantic taken by the *Gerda, Pillsbury* and *Oregon*, three have 9 arms, all the rest 10, though Madsen (1950) found 2 of the 37 *Atlantide* specimens to have 9 arms and another only 8.

A species of *Luidia* with usually 10 arms, relatively slender and attenuated; abactinal paxillae all relatively small and rounded but rather variable in size medially, some slightly larger ones intermingled; laterally two matching longitudinal series each side, outnumbering the adjacent more elongate superomarginal paxillae by 15–18/10; inferomarginal plates mainly lateral in alignment, bearing up to four spines in *L. heterozona barimae* but rarely more than three in *L. heterozona heterozona*, the spines erect, long and acute, the uppermost (at least on alternate plates) projecting vertically upwards and the uppermost or the second the longest, the spines alternating fairly regularly in level on successive plates and often also in number 4/3 or 3/2, the plates unusually bare of spinelets between the large spines except at the edges; actinal plates unusually elongate, partially overlying the abradial ends of the adambulacrals; adambulacral plates mostly with three spines in line at right angles to the furrow but in larger specimens, R>70 mm, *c.* 10–15 proximal plates may have a fourth spine enlarged proximal to the abradial one; pedicellariae bivalved throughout, often very abundant, especially on the paxillae (Fig. 3j) where they are relatively short and rounded, their edges almost fully contiguous, actinal pedicellariae longer, sometimes broadened at the tips, numbering up to three on some proximal actinal plates, similar ones on the inferomarginals and oral plates while one to three more spiniform pedicellariae also occur on the furrow face of each oral plate near the mouth. Colour in life dark chocolate brown above except for a white band along the upper edge of each arm (possibly the superomarginals), the inferomarginal spines white with brown bases.

STATUS OF *L. barimae*. *Luidia barimae* was established on the basis of two poorly preserved specimens from off Venezuela. Walenkamp (1976) has recorded nine others from Surinam, evidently also in poor condition. About 50 further specimens from the *Pillsbury* collections off the north coast of South America have now been studied, as well as more than 100 from West Africa of *L. heterozona.* Though many of these are also poor, some are good enough to show that there are two matching regular longitudinal series of lateral paxillae adjacent to the superomarginal paxillae in the american and well as african specimens. Also the superomarginal paxillae are similarly markedly larger than the other paxillae (Fig. 2f). This leaves only the number of inferomarginal spines as a possible distinction between the two, *L. barimae* being described as having four spines proximally, then three, whereas no more than three, more often three and two, are said to be found in *L. heterozona* by Fisher, Madsen and Cadenat. However, one large *Pillsbury* specimen from the Gulf of Guinea, West Africa, with R at least 150 mm, was found to have four inferomarginal spines on a few proximal alternate plates, while conversely a specimen from Venezuela with R *c.* 120 mm has no more than three spines, though these reduce to two on the alternate distal plates. Certainly there is no justification for more than a subspecific distinction between specimens from the two sides of the tropical Atlantic and the minor difference in the marginal spines is clearly correlated with different growth rates.

DISTRIBUTION. *L. heterozona heterozona* from Cap Blanc, Mauritania, south to Elephant Bay, Angola; 28–975 metres. As noted above (p. 163), apart from Sibuet's Walda Expedition record (1975), the greatest depth recorded is 400 metres.

L. heterozona barimae from off the Gulf of Maracaibo, western Venezuela (*c.* 12°34′ N : 71°10′ W) eastwards to French Guiana (06°07′ N : 52°19′ W); 38–90 (?100) metres.

Luidia ludwigi scotti Bell
Figs 2a, e, 3t, u

Luidia scotti Bell, 1917 : 8–9; A. M. Clark, 1953 : 383–385, fig. 3, pl. 40, fig. 1; John & A. M. Clark, 1954 : 144; Carrera-Rodriguez & Tommasi, 1977 : 62, 65–66.
Luidia doello-juradoi Bernasconi, 1941 : 117; 1943 : 8–11, pl. 1, fig. 3, pl. 2, figs 2, 3, pl. 3, figs 4, 5.
Luidia rosaurae John & A. M. Clark, 1954 : 142–145, figs 1, 2, pl. 6, fig. 1; Jangoux, 1978 : 95.
Luidia ludwigi: Walenkamp, 1976 : 32–37, fig 9, pl. 2, figs 1, 2, 4, pl. 4, fig. 3.

R up to 90 mm; R/r 5·3–8·1/1, mean of 9 specimens 7·0/1.

A species of *Luidia* with normally 5 arms: abactinal paxillae with two longitudinal rectangular or squarish lateral series each side, matching each other and also the adjacent slightly smaller superomarginal paxillae, central paxillar spinelets distinctly coarser than the peripheral ones and in smaller specimens, R < *c.* 40 mm, where the median paxillae often have only a single central spinelet, this may stand out from the surface slightly but not as much as in *L. sagamina*; larger specimens with multiple central spinelets have them relatively shorter and making a uniform surface; inferomarginal plates mainly ventral in alignment, bearing one or two (in the largest specimens, R *c.* 90 mm, sometimes three) stout ambital spines, the upper one more or less shorter than the lower when there are two, on the ventral side 4 or 5 much smaller, almost cylindrical, but slightly tapering spines; adambulacral plates with 4 large spines, the abradial two in line parallel to the furrow; pedicellariae 3- or 4-valved on at least the more proximal actinal plates, the valves varying in shape from broadly spatulate to evenly tapering and triangular (see Fig. 3t, u), sometimes bivalved pedicellariae present on the paxillae and inferomarginal plates, absent from the furrow face of the oral plates. Colour (recently dried) patterned above with dark rose-coloured patches on the centre of the disc and bands across the arms, sometimes linked by continuous colour midradially.

SYNONYMY. The poorly-preserved holotype and two paratypes of *Luidia rosaurae* John & Clark, 1954, from off Venezuela, were thought to differ from *L. scotti* Bell, 1917, of southern Brazil in having only a single large ambital inferomarginal spine, finer ventral armament and more numerous pedicellariae. Walenkamp's material from Surinam (1976) and a number of *Pillsbury* and *Gerda* specimens from northern South America and the Florida Strait now studied, show that there is considerable variation in the development of the second (upper) inferomarginal spine, the thickness of the ventral spines and the frequency of the pedicellariae; consequently *L. rosaurae* cannot be maintained as specifically distinct. Walenkamp deferred a decision on this point in default of material from the type locality of *L. scotti*. Simultaneously, he rejected the synonymizing of *Luidia doellojuradoi* Bernasconi, 1941 with *L. scotti*, proposed by A. M. Clark (1953), on the grounds that its marginal paxillae are larger than the lateral ones and the R/r ratio is only 7/1. However, he was misled in this by Bernasconi's peculiar terminology of the lateral and superomarginal paxillae (see p. 166), the true superomarginal paxillae of *L. doellojuradoi* being in fact smaller than the lateral ones. Also in the 15 *Terra Nova* specimens of *L. scotti* the R/r ratio ranges upwards from 7/1; in the lectotype (incorrectly called holotype in 1953) it is 7·5/1. Thanks to Dr Bernasconi, there are two specimens which she named as *L. doellojuradoi* in the British Museum collections. Apart from the greater extent of the actinal pedicellariae on the arms and the occurrence of some inferomarginal pedicellariae—characters not considered to be of specific weight—no significant differences from *L. scotti* are apparent. The ventral armament of the inferomarginal plates has become appressed during preservation, which lends a rather coarser appearance than is shown by the well preserved type material of *L. scotti*.

It is also possible that *L. patriae* Bernasconi will prove to be synonymous with *scotti*.

Walenkamp (1976) percipiently noted the close affinity between *L. ludwigi* Fisher, 1906, from California and specimens from the north coast of South America conspecific with *L. rosaurae*, referring the latter to the synonymy of *L. ludwigi*. Fisher's holotype has R 110–115 mm and superficially resembles the larger Atlantic specimens seen except that it is rather coarser. A paratype of *L. ludwigi* with R 72 mm compares closely with a paralectotype of *L. scotti* of almost the same size but there appears to be a significant difference in the number of paxillar spinelets, the median paxillae of *ludwigi* rarely having less than 6 coarse ones whereas in *L. scotti* the number is most often only about 3. Possibly there is also a colour difference, Fisher having described *L. ludwigi* (at least when freshly preserved) as being reddish above 'sometimes mottled with lighter', whereas Atlantic specimens seem to be more boldly patterned dark (?red) and light. In conjunction with the geographical difference, these small differences are now considered to warrant a subspecific distinction.

One further nomenclatural threat still remains. Döderlein (1920), in listing *L. ludwigi*, noted that it is possibly (vielleicht) a synonym of *L. armata* Ludwig, 1905, from the Gulf of Panama. Accordingly, one of the two intact syntypes of *L. armata* from the U.S. National Museum has been studied; it has R 47 mm and is slightly decalcified and flaccid. The armament of the paxillae is more or less appressed, emphasizing the spiniform shape of the central spinelets. Although the larger Pacific specimens of *L. ludwigi* have markedly coarser and shorter central spinelets, tending to appear granuliform, smaller Atlantic specimens from the vicinity of Florida with R *c.* 40 mm, have a very similar relatively elongate armament and also agree in the shape and arrangement of the paxillae, plates and spines. However, the syntype of *L. armata* differs in having a very large, highly modified bivalved pedicellaria on each oral plate—a feature somehow overlooked by Ludwig and not found in the type material of *L. ludwigi* seen or any Atlantic specimens. It also has relatively small actinal interradial areas with no sign of a second row of actinal plates. At R 40 mm, *L. scotti* already has a single median interradial actinal plate distal to the main series and in larger specimens, R 50–60 mm, there are one or two such plates each side of the interradius. These two characters, but particularly the first, indicate that there are two distinct species in the East Pacific.

DISTRIBUTION. Eastern Gulf of Mexico west of Florida, (*c.* 27½° N : 84° W) and Florida Strait, also the northern and eastern coasts of South America from Venezuela to northern Argentina (*c.* 39° S); 33–126 (?135) metres. The northernmost record from 85 miles west of St.Petersburg, Florida, is thanks to Dr. K. Serafy and with seven *Gerda* stations in the Florida Strait provides a considerable extension of the range from South America. About 35 specimens from 12 *Pillsbury* stations came from Venezuela to French Guiana and also served to extend the bathymetric range both up and down, the three shallowest—33, 36 and 42 metres—being from Surinam and French Guiana. There is also a specimen labelled as being from *Pillsbury* st. 1384, which is in the Puerto Rico Trench (*c.* 19°45′ N : 67°00′ W) at 7956 metres! Although it has relatively long arms (R/r 65/8 mm = 8·1/1), about the maximum found in *scotti*, the paxillar structure, form of the pedicellariae, general armament and banded colour pattern leave no doubt of the identification, but the locality is evidently a mistake.

Ludia patriae Bernasconi

Luidia patriae Bernasconi, 1941 : 117–118; 1943 : 11–13, pl. 1, figs 1, 2.

R 72 mm (holotype); R/r 7·2/1.

A species of *Luidia* with normally 5 arms; abactinal paxillae with the two lateralmost series forming transverse rows with the matching superomarginal paxillae and all rectangular or squarish in shape: inferomarginal plates mainly ventral in alignment, bearing two slightly flattened and slightly curved large spines near their upper ends at the ambitus, the lower one larger, and on the ventral side about six pointed spines, cylindrical or somewhat flattened; adambulacral plates with four large spines, the two abradial ones in line parallel to the furrow: pedicellariae absent throughout. Colour (dried) dark rose above with darker areas in the centre of the disc and on the median parts of the arms.

AFFINITIES. *L. patriae* is very similar to *L. ludwigi scotti*, of which Bernasconi had as many as 80 specimens (as *L. doello-juradoi*), though only six or seven of *L. patriae*, which she supposed to differ in the absence of pedicellariae (not now thought to be a character of specific weight), the form, number and arrangement of the ventral inferomarginal spines and in lacking the two or three enlarged spinelets abradial to the four main adambulacral spines described for *L. doello-juradoi*. Possibly *L. patriae* will also prove to be a synonym of *L. ludwigi scotti*.

DISTRIBUTION. Northern Argentina. 34½–37½° S [?also from Uruguay, 33°S]; 100–126 metres.

Luidia sagamina aciculata Mortensen
Fig. 1d, 2k, 3l, s

?Luidia alternata bicolor Verrill, 1915 : 203, pl. 12, fig. 1.
Luidia sagamina: Downey, 1973 : 24.
Luidia aciculata Mortensen, 1933*b* : 425–426, fig 7, pl. 20, figs 7–12; Fisher, 1940 : 268–269, fig. M5; Nataf & Cherbonnier, 1973 : 80–82, pl. 3, figs A, B, pl. 6, figs 1–6, pl. 9, figs G, H: Sibuet, 1975 : 284, 288.
Luidia sagamina var. *aciculata*: Madsen, 1950 : 199–203, figs 6, 7.
Luidia sagamina aciculata: A. M. Clark, 1955 : 33; A. M. Clark & Courtman-Stock, 1976 : 23, 32, 45.
Luidia atlantidea: Downey, 1973 : 25 [Non *L. atlantidea* Madsen, 1950.]

R up to 140 mm; R/r 7·0–10·5/1.

A species of *Luidia* with normally 5 arms; abactinal paxillae all with an enlarged median spinelet (sometimes replaced by a pedicellaria) both stouter and longer than the remaining spinelets; two (or in the largest specimens three) longitudinal series of lateral paxillae also matching transversely but outnumbering the much longer superomarginal paxillae by 16–19/10; inferomarginal plates mainly lateral in alignment, bearing two or three, sometimes four large spines, tending to alternate in number and position on consecutive plates, the uppermost spine the longest and projecting vertically upwards in its natural position, at least on every second plate; adambulacral plates with two or three large spines in a line at right angles to the furrow, when only two, the abradial one is relatively large; pedicellariae usually present on at least the proximal actinal plates, where they are more or less broadened basally and tapering so that the individual valves are triangular, though not closely contiguous except terminally, abactinal pedicellariae bivalved and shorter, sometimes absent but one or more elongate bivalved pedicellariae always present on the furrow face of each oral plate near the mouth, though not fully developed from spinelets in small specimens. Colour in life purple to purple-brown above, white below, marginal spines dark brown basally.

SYNONYMY. Madsen (1950) decided that *Luidia sagamina* Döderlein, 1920 from Japan and *L. aciculata* Mortensen, 1933 from St Helena are conspecific, following comparison of Mortensen's type material with a specimen from Sagami Bay and others collected off West Africa by the *Atlantide*. Although he retained *aciculata* as a subspecies, he could not find any real difference between it and *sagamina*. This prompted Downey (1973) to drop *aciculata* and use *L. sagamina* for some american specimens, though conversely Nataf and Cherbonnier in the same year retained *aciculata* at the specific level, without explanation. Madsen had also referred to *L. sagamina aciculata* a specimen from Durban, Natal and in 1976 (Clark & Courtman-Stock) I retained this terminology, though without having seen any specimens from either Japan or Natal. Since then, further echinoderm material from off Natal (A. M. Clark, 1977) has shown that the fauna of SE Africa has much in common with that of southern Japan and the East Indian area. This would imply that the Durban specimen should be named *L. sagamina sagamina* if two subspecies are to be recognized, as seems desirable to me in the absence of precedent from related species of moderate depths common to similar areas of the Atlantic and Indo-West Pacific.

A further complication is raised by the possibility that *Luidia sagamina aciculata* is conspecific with the (two?) specimens from the Florida Strait which Verrill (1915) called *Luidia alternata* variety *bicolor*. Verrill's drawings show relatively small single spines (or enlarged spinelets) on *all* the abactinal paxillae, quite different from the sporadic and much larger spines of *L. alternata*. Also the lateral paxillae outnumber the inferomarginal plates (the superomarginals were not distinguished by the artist) and the inferomarginal spines are regularly alternating on consecutive plates, as in *L. sagamina* and *aciculata*. Downey (1973) recorded a small specimen (R in fact 21 mm not 8 mm as given in her paper) from South Carolina as *L. sagamina* and mentioned another (p. 25) which she referred to *L. atlantidea* because of light lateral bands along the arms but which also proves to be conspecific with the first. A further specimen, R 24 mm, from *Gerda* st. 1039 in the Florida Strait may be

Halpern's supposed *L. atlantidea*, mentioned by Downey. Unfortunately the Bahama Expedition's specimens of *L. alternata* var. *bicolor* cannot now be found at the University of Iowa. Since the revival of *bicolor* as a specific name would mean that both *L. sagamina sagamina* and *aciculata* became junior synonyms and there is an element of doubt about the identity, it is desirable that the name *bicolor* should be formally set aside.

Verrill's specimens evidently had only two adambulacral spines, which is also the case in the small *Silver Bay* and *Gerda* specimens. Mortensen's holotype of *L. aciculata* from St. Helena, Fisher's *Discovery* specimen from off the Congo (Zaire), a *Pillsbury* specimen from the Gulf of Guinea (Fig. 2k) and an *Atlantide* west african specimen all usually have three adambulacral spines. Unfortunately, Madsen recorded four other *Atlantide* specimens with only two such spines and this is also true of two other *Pillsbury* Guinea specimens. Clearly, this character of adambulacral armament cannot be used to distinguish yet another american, as opposed to african, subspecies, comparable to the subspecies of *L. heterozona* and *L. alternata*, which would make for consistency of taxonomic treatment. The present american specimens are too small and too few to suggest other possible differential characters.

DISTRIBUTION. North Carolina to south and west Florida and from Cap Blanc, Mauritania south to Zaire and from St. Helena, 20–975 metres. As noted above (p. 163), apart from Sibuet's Walda Expedition record (1975), the greatest depth recorded is 150 metres.

Luidia sarsi Düben & Koren
Figs 1c, 2c, g, 3m–o, v, 6

Asterias sp. aff. *A. aranciaca*: M. Sars, 1835 : 39.
Luidia fragilissima (pt, five-armed specimens) Forbes, 1841 : 135–140.
Luidia Sarsii Düben & Koren, 1845 : 113; Perrier, 1875 : 342 [1876 : 262]; Sladen, 1889: 258; Süssbach & Breckner, 1911 : 210.
Luydia Savignyi (pt) Düben & Koren, 1846 : 254, pl. 8, figs 23, 24.
Luidia elegans Perrier, 1875 : 336–337 [1876 : 256]; 1884 : 269[?], pl. 10, fig. 7 [and probably also fig. 8], captioned '*L. barbadensis*'; Verrill, 1885 : 543, pl. 13, fig. 39; 1915 : 203–205, pl. 16, figs 4, 4a, pl. 19, fig. 1; Döderlein, 1920 : 289–290, fig. 36; Gray, Downey & Cerame-Vivas, 1968 : 140, fig 9; Downey, 1973 : 25, pl. 3, figs C, D; Blake, 1973 : 40–41, pl. 10, figs 27–52; Carrera-Rodriguez & Tommasi, 1977 : 71–75, figs 10–12.
Astrella simplex Perrier, 1882 : 21, fig. 25; 1894 : 193–194, pl. 14 , fig. 3.
Luidia africana Sladen, 1889 : 256–258, pl. 44, figs 1, 2, pl. 45, figs 1, 2; Koehler, 1923 : 132; H. L. Clark. 1923 : 252; 1925(pt) : 8; Mortensen, 1933*a* : 239–240, figs 3, 4; Madsen, 1950(pt) : 188–192, fig. 4, pl. 16, figs 3, 4; A. M. Clark, 1952 : 195; 1953 : 393–394, figs 10, 11; Nataf & Cherbonnier, 1973 : 79, pl. 8; A. M. Clark & Courtman-Stock, 1976 : 23, 30, 44, fig. 26. [Non *L. africana*: Koehler, 1911 : 19; Döderlein, 1920 : 228, nec Mortensen, 1925 : 178 = *L. atlantidea*.]
Luidia sarsi: Bell, 1893 : 72; Koehler, 1895 : 320, pl. 9, figs 6, 7; Ludwig, 1897 : 85–104, pl. 4, figs 2, 3, pl. 7, figs 1–12; Koehler, 1909 : 59; Döderlein, 1920 : 288–289, fig. 35; Koehler, 1921 : 57, fig.; Mortensen, 1925 : 178 [?*sarsi* acc. Madsen, 1950]; 1927 : 69, fig. 39b; Tattersall & Sheppard, 1934 : 36–55 (larvae); Madsen, 1950 : 187; Tortonese, 1965 : 150–152, fig. 69. [Non *L. sarsi*: Studer, 1884, = *L. africana* acc. Döderlein, 1920 but much more likely = *L. atlantidea*.]
Luidia paucispina von Marenzeller, 1893 : 3–4, pl. 1, fig. 1.

SIZE. The maximum size varies in different parts of the range. In NE Atlantic specimens (*L. sarsi sarsi*) R reaches only *c.* 110 mm (BM coll., W of Scotland) but the same subspecies from the Mediterranean, *L. sarsi africana* from South Africa and *L. sarsi elegans* from America may reach 180–190 mm R; R/r 5·0–10·5/1, usually 7·5–10·0/1 at R>90 mm.

DIAGNOSIS. A species of *Luidia* with normally 5 arms, becoming long and evenly tapering in large specimens, R>90 mm, but somewhat petaloid in smaller ones; abactinal paxillae relatively small and rounded, with two matching slightly coarser longitudinal lateral series each side but these are inconspicuous, outnumbering the markedly elongate superomarginal paxillae by 17–20/10, paxillar armament of fine spinelets of fairly uniform length, median paxillae mostly with only a single central spinelet, sometimes distinctly coarser in *L.*

sarsi sarsi where the peripheral spinelets are also less attenuated than in *L. sarsi africana* and *L. sarsi elegans* (see Fig. 3m, n, o); inferomarginal plates mainly lateral in alignment, bearing 2–4 usually 3, large pointed spines, showing some tendency to alternate in position and number on successive plates, the two upper spines similar in length, the uppermost often longer when not at its highest position; actinal plates distinctly broadened and keeled transverse to the arm axis; adambulacral plates with three large spines in series transverse to the furrow and sometimes one (or two) enlarged spinelets proximal to the lateralmost; pedicellariae bivalved with fairly broad rounded tips, usually almost circular in cross section but the valves sometimes rather flattened towards the tips, common on the median abactinal paxillae of *L. sarsi africana* and *L. sarsi elegans*, occasional in *L. sarsi sarsi* but longer actinal pedicellariae usually present in all three subspecies proximally, with one on the furrow face of each oral plate (exceptionally represented by two hardly modified spines). Colour in life brownish yellow, reddish or orange above, pale below, arms medially and marginal plates darker, especially in *L. sarsi africana*.

STATUS OF *L. africana* AND *L. elegans*. These two taxa of Sladen, 1889 and Perrier, 1875 are here regarded as conspecific with *L. sarsi*.

Confusion in the limits between *L. sarsi* and *L. africana* has arisen because the type material of the latter included one specimen from Atlantic Morocco besides the main sample from South Africa, one of the latter conforming to the size and description given by Sladen, as I noted in 1953 (p. 393). The moroccan specimen has fairly numerous globose pedicellariae on the abactinal paxillae, as in the southern specimens. Although such pedicellariae were thought to be rare in north european specimens of *L. sarsi*, some larger specimens from west of Scotland collected since 1953 were found to have more or less numerous pedicellariae (Fig. 3m), sometimes two or three on a single paxilla. It is significant that there are no reliable identifications of *L. africana* from any localities between Cape Verde and Luderitz Bay, Namibia. Despite a critical comparison by Nataf & Cherbonnier (1973) out of 213 five-armed specimens of the *ciliaris*-group (excluding *L. sagamina aciculata*) from this area, every one was found to be referable to *L. atlantidea* and not to *L. africana*. Döderlein's record (1920) of *L. africana* from the Cape Verde Islands (based on two specimens named *L. sarsi* by Studer in 1884) is clearly in mistake for *L. atlantidea* since he particularly notes the relative coarseness of the central paxillar spinelets and the occurrence of pedicellariae on the superomarginal but not the abactinal paxillae—the reverse of what is found in *L. africana*, where both central and peripheral paxillar spinelets are uniformly fine. Madsen (1950) has referred Mortensen's larger moroccan specimens also to *L. atlantidea*, leaving under the heading of *L. africana* only some smaller moroccan ones which 'might just as well belong to *L. sarsi*' and three fragmentary *Atlantide* specimens which 'are not immediately recognizable as *L. africana*'. Zoogeographically, it would be expected that the distribution of a northern species also found in the Mediterranean, could well extend southwards to some extent in north-west Africa, as with *Marthasterias glacialis*, for instance, which also occurs in South Africa but is unrecorded between Cape Verde and Cape Town.

There are in the British Museum collections six specimens from near Cap Blanc (*Discovery* stations 8005 and 8020, 101 and 261–297 metres) with R 32 to *c.* 140 mm. These are certainly not *L. atlantidea*, having uniformly fine paxillar armament, abactinal rather than superomarginal pedicellariae, no white lines emphasizing the positions of the superomarginals but darker brown midlines to the arms, much as in *L. sarsi* and *L. africana*. These specimens are a little unusual in having the pair of lateral spines on the furrow face of each oral plate hardly modified, if at all, into a pedicellaria. One exception is the smallest one, surprisingly since it is usually in larger specimens of species such as *L. heterozona* that this pedicellaria is more modified. Nearly all the specimens of *L. sarsi, africana* and *elegans* seen have quite a well-developed oral furrow pedicellaria, though the two spines from which it is modified may be more or less unequal in size. A second feature of some of these Cap Blanc specimens is that some proximal superomarginal paxillae are unusually broad, almost square, rather than consistently elongated, squarish paxillae being a characteristic of *L.*

atlantidea. This is naturally limited to the plates adjacent to those inferomarginals where the highest spine is not at the upper edge of the plate.

In describing *L. africana*, Sladen (1889) cited seven supposed differences from *L. sarsi*, the larger size (R up to 160 mm in the type material), the more even taper of the arms, the smaller size of the median paxillae, the lesser prominence of the central median paxillar 'granule' (spinelet), the greater length of the uppermost inferomarginal spine relative to the second spine, the greater length of the third (lateralmost) adambulacral spine, achieving equality with the second spine, and the less pointed form of the actinal pedicellariae. Subsequently Madsen (1950) noted that abactinal pedicellariae are not only much more often found in *L. africana* than in *sarsi*, where they are rare, but also that their position, when present in *sarsi*, is peripheral, while those of *africana* are central on the paxillar tabulum, so that the pedicellariae of *sarsi* tend to be seen in profile rather than from the top. He also noted that the inferomarginal spines of *L. africana* differ in having dark pigmented skin basally.

As far as size is concerned, although in Norway, the type locality of *L. sarsi*, larger specimens usually have R only 50–60 mm, around Scotland it may reach *c.* 110 mm and in the Mediterranean reputedly *c.* 180 mm (diameter 35 cm). Such larger specimens also have the arms more attenuated and evenly tapering and there is greater disparity in the size of the additional median paxillae. As for the relative lengths of the inferomarginal and adambulacral spines, these are dependent to some extent on growth, the lateralmost adambulacral spine being retarded in growth relative to the second spine, while it would be more correct to say that the two upper inferomarginal spines of *L. sarsi* are similar in length, the uppermost one often slightly longer, especially on those plates where it is not in its highest position, as is the case in the lectotype now proposed (see below), even though R is less than 40 mm. At R 100+ mm the third spine approximates in length to the other two in specimens from all localities, a characteristic thought by Döderlein (1920) to be diagnostic of *L. elegans*.

With regard to the occurrence of abactinal pedicellariae, in 1953 I noted that in four out of ten northern specimens of *L. sarsi* studied, some pedicellariae were present. As mentioned above, subsequent scottish collecting has yielded material with pedicellariae as numerous as in the moroccan paratype of *L. africana* and some south african specimens. In 1953 I also contended that the pedicellariae are not really central on the paxillae of *L. africana* (or *L. elegans*) either but that this may appear so when the paxillae are crowded in preservation and the valves are coarser, pushing the pedicellariae into a more nearly vertical alignment on the tabulum. There is rarely a complete circlet of spinelets, as shown in Mortensen's fig. 3 (1933*a*) and Madsen's fig. 4c, d (1950). The shape of the pedicellariae, both abactinal and actinal ones, varies to some extent in different specimens from both north and south. Viewed end-on, the outline is usually approximately circular and the shape appears globular but may be slightly oval in one plane or the other if the valves are either thickened or broadened. The very broad shapes of both kinds of pedicellaria shown in Madsen's fig. 4h, i and k (1950), the abactinal ones cockle-shaped and the actinal ones with the individual valves bat-shaped (fan-shaped according to Madsen) seems to be exceptional even among south african specimens, none of the ten now studied having such an exaggerated form. Usually their actinal pedicellariae are either tapered in both side views (like a bishop's mitre) or else the tips are blunter and often thicker, a range also shown by northern specimens.

Finally, the shape of the abactinal paxillar spinelets needs to be compared. In many northern specimens of *L. sarsi* the majority of median paxillae do have the single central spinelet distinctly coarser than the peripheral ones, appearing almost granuliform as foreshortened. This is particularly, but not exclusively, true of smaller specimens, including the lectotype, but in other specimens the thickness of all the paxillar spinelets is similar. A comparable modification of the central paxillar spinelet is noted above in some smaller specimens of *L. ludwigi scotti* and of course in a much more exaggerated form in *L. sagamina aciculata*, where the central spinelet is more or less markedly elongated as well as being much thicker than the peripheral spinelets. In general, the paxillar spinelets of south african specimens are appreciably more attenuated than those of european specimens and none have been observed to show a coarsening of the central spinelet, though it should be emphasized that no specimens with $R < 70$ mm are available.

To sum up, in comparison between specimens from South Africa and those from Europe and NW Africa, no differences of specific weight can be found. There are slight differences in the armament of the paxillae in some specimens, the southern ones tending to have a finer and more uniform armament but this seems to be shared by some moroccan specimens and is always very subtle. Although the frequency of pedicellariae seems to increase further south, only in occasional south african specimens with extremely broad pedicellariae are these organs distinctive. It is therefore doubtful whether the name *africana* is worth retaining for a subspecies from South Africa but the distribution gap in west Africa coupled with these minor morphological differences may justify it.

With regard to *Luidia elegans* from the american side of the Atlantic, the only comparison given by Perrier was of the ventral side with that of *L. alternata* just described, the difference emphasized being the bivalved rather than trivalved pedicellariae. In Döderlein's key (1920), he distinguished *L. elegans* from the much more closely related *L. sarsi* and *L. africana* by the equal length of all three inferomarginal spines being supposedly limited to *L. elegans*, which was also said to be the only one to have numerous paxillar pedicellariae. This comparison was evidently made primarily on the evidence of a single small specimen of *L. sarsi* (R 29 mm), one of *L. elegans* with R 145 mm and two specimens from the Cape Verde Islands which he thought to be *L. africana* but are more likely *L. atlantidea*. Inevitably, in smaller specimens the lowest inferomarginal spine, if developed at all, is relatively smaller, while at most stages of growth the two upper spines are similar in length, as discussed above. At R *c.* 100 mm in European specimens all three spines may be about equal, while the occurrence of pedicellariae is clearly variable and of little taxonomic weight.

However, there does appear to be a significant difference in the number of abactinal paxillae across the arm, at least in smaller specimens, R 40–50 mm, on the two sides of the Atlantic. Excluding the two series of superomarginal paxillae, the number in american specimens of about this size is proximally *c.* 13 compared with *c.* 17 in those from the East Atlantic. Unfortunately, owing to their irregular arrangement, it is difficult to make a precise estimate of the number of paxillae, especially in larger specimens. Also, the limited amount of material available indicates that the paxillar number may increase at a higher rate in american specimens. There is a small degree of support for this character in the armament of the adambulacral plates. At R *c.* 40 mm, the third (lateralmost) spine is much smaller than the second in american specimens and even at R 70 mm this spine is still much narrower basally than the second and only about two-thirds as long. Only when R approaches 140 mm does the third spine achieve parity in magnitude with the second on most plates. As for the accessory adambulacral spinelets, in specimens from both sides of the Atlantic one (sometimes two) is usually somewhat enlarged proximal to the third spine (or the space between second and third spines). This spinelet is usually one-third to half, but occasionally as much as three-quarters as long as the third spine. In american specimens this accessory spinelet(s) remains slender but in the eastern Atlantic can be basally stouter and more conical in shape. However, there is so much variation in the adambulacral armament that these differences cannot be of much importance. Finally, the madreporite may remain obscured by the paxillae to a greater extent in specimens from the eastern Atlantic than in american ones but this is probably correlated with size (the plate becoming more prominent in larger specimens) and is affected by preservation. In total, these minor differences do not add up to more than a subspecific distinction between *L. elegans* and *L. sarsi*.

Finally, Koehler (1923) and Carrera-Rodriguez & Tommasi (1977) have recorded specimens from Uruguay (33° S) and southern Brazil (*c.* 30½° S) as *L. africana* or *L. elegans*. Because of the great geographical discontinuity between them and the rest, comparable to that between *L. sarsi sarsi* and *L. sarsi africana*, it is not improbable that a minor morphological difference justifying a taxonomic distinction of eastern south american specimens may exist, most likely again at the subspecific level.

LECTOTYPE. Because of the complex affinities of *Luidia sarsi*, it seemed desirable that a lectotype be selected from among Sars' material from Bergen to which Düben & Koren gave this name in 1845. Thanks to Dr M. E. Christiansen of the Zoologisk Museum, Oslo, it is clear that no type was designated at the time. The specimen chosen (one of seven) was from Manger, near Bergen, Oslo Museum reg. no. E1005a, shown in Fig. 6.

R (maximum)/r is 37/8 mm, = 4·6/1. The shorter arms have R 30 and 32 mm. (The relatively low R/r ratio is to be expected at this relatively small size.) About 17 lateral paxillae correspond to 10 of the more proximal superomarginal paxillae. The median paxillae nearly all have a single, slightly coarser, central paxillar spinelet and usually 7–11 peripheral spinelets. Excluding the superomarginal ones, there are *c.* 17 paxillae across the arm breadth basally. The paxillae of the outer lateral row have up to three central spinelets.

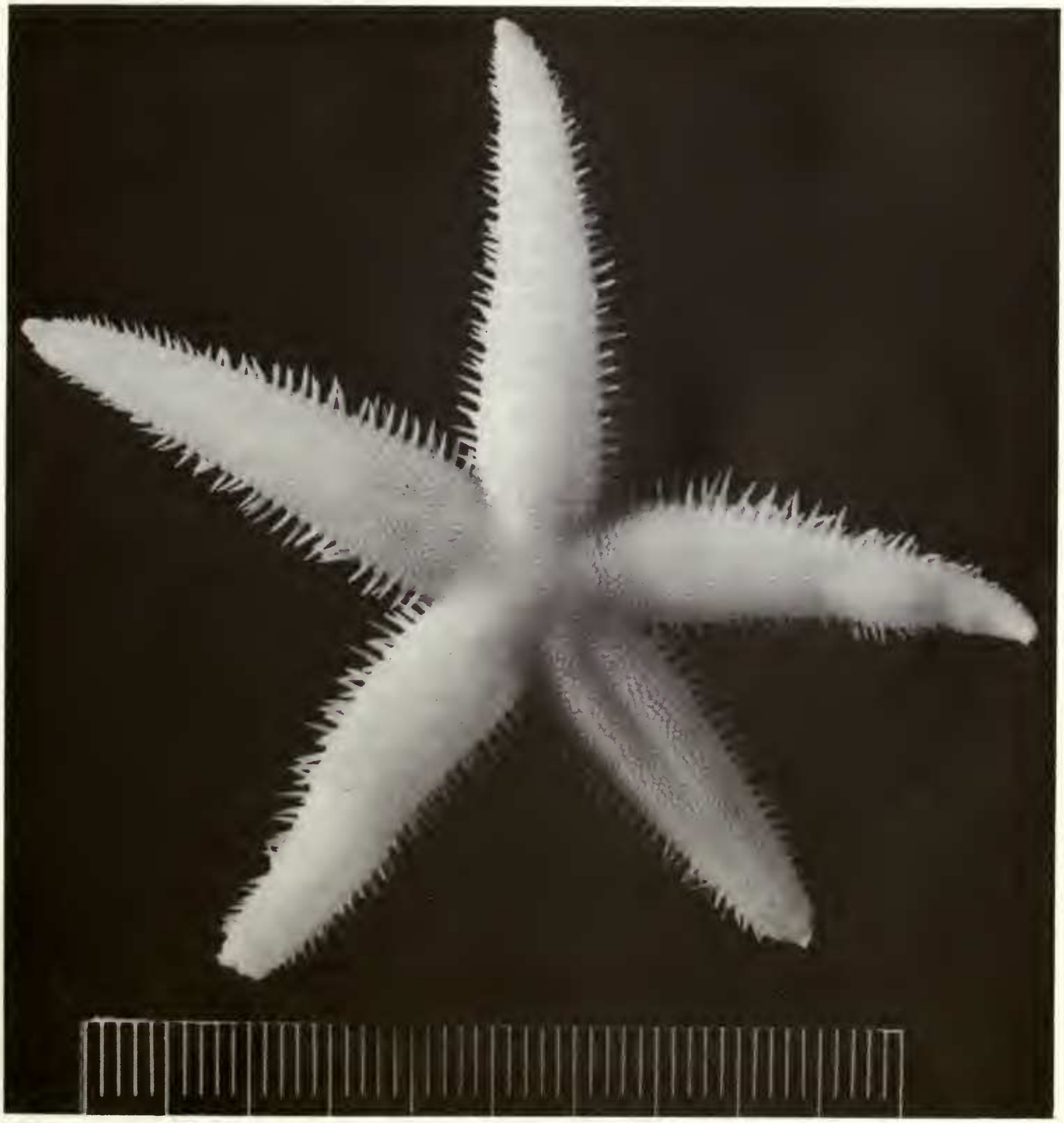

Fig. 6 *Luidia sarsi sarsi* Düben & Koren, lectotype, Zoologisk Museum, Oslo reg. no. E1005a, Manger, near Bergen. Dorsal view, × 2·2.

All the spinelets of the lateral paxillae are distinctly coarser than those of the median ones, while the superomarginal armament is coarser still. The madreporite is not distinguishable. The inferomarginal plates bear 2–4 large spines, rather variable in level on the plate, sometimes alternating, though at the same level on several consecutive plates. The uppermost spine is usually slightly the longest. Most proximal actinal plates bear a single blunt, bivalved pedicellaria but no abactinal pedicellariae were observed. Each adambulacral bears 3 large spines and an enlarged spinelet one-third to half as long as the lateralmost one and proximal to it. Each oral plate bears about four large spines in an abradial row and one other spine near the furrow margin, besides a large bivalved pedicellaria in the furrow.

The paralectotypes include four smaller specimens and two larger but broken ones, one with R *c.* 50 mm and the other R/r 55/9·5. The central spinelet of the median paxillae is also distinctly coarser than the peripheral ones; *c.* 20 lateral paxillae correspond to 10 superomarginal ones; proximally there are usually four inferomarginal spines.

Holotype of *Luidia elegans*. Because of Perrier's rather inadequate description, this specimen was borrowed for reexamination from the Museum of Comparative Zoology, Harvard. The number is M.C.Z. 372. It proved to be in fact the specimen illustrated in Perrier, 1884, pl. 10, fig. 7, under the name of *L. barbadensis*, though the negative was reversed in printing. One arm is abnormally short, probably regenerated, and curled up at the tip. R is *c.* 40 mm for the longest arm (Perrier gives 35 mm); r is 7 mm; 18 lateral paxillae correspond to 10 superomarginal ones; proximally there are *c.* 13 paxillae across the arms between (but not counting) the superomarginal ones. The median paxillae mostly have only a single central spinelet, not at all coarser than the peripheral ones. No abactinal pedicellariae were seen. Most inferomarginal plates bear three large spines, sometimes two, showing a tendency for alternation in position. The actinal pedicellariae are bivalved and blunt-tipped. The third adambulacral spine is reduced on some plates. The locality is 'Straits of Florida, 101 fathoms'. Verrill's guess that Perrier's '101 brasses' meant *feet* being incorrect.

Distribution. *L. sarsi sarsi* from Trondheim Fjord, Norway to Cap Blanc, Mauritania, the Azores and the Mediterranean; 9–1300 metres.

L. sarsi africana from Luderitz Bay to the Port Elizabeth area of South Africa; 54–360 metres.

L. sarsi elegans from east of New Jersey, U.S.A. (*c.* 41° N) to the Florida Strait and both east and west Gulf of Mexico; also from southern Brazil (*c.* 30½° S) to Uruguay (*c.* 33° S); 60–365 metres. There are no reliable records from the caribbean, Perrier's supposed specimens from Barbados being untraced in the M.C.Z. and it is significant that no specimens appear to have been taken by the intensive collections of the *Atlantis* around Cuba (H. L. Clark, 1941) or by the *Pillsbury* in the caribbean, Lesser Antilles or north of South America.

Luidia senegalensis (Lamarck)

Asterias senegalensis Lamarck, 1816 : 567.

Luidia senegalensis: Müller & Troschel, 1842 : 78, pl. 5, fig. 4; Perrier, 1875 : 342–343 [1876 : 262]; Döderlein, 1920 : 249–250, figs 9, 20; H. L. Clark, 1933 : 20–22; Bernasconi, 1943 : 5–6; Tommasi, 1958 : 9–11, pl. 2, fig. 2; Ummels, 1963 : 94–95, pls 10, 11; Downey, 1973 : 22, pl. 1, figs A, B; Blake, 1973 : 30, pl. 2, figs 1–31; Walenkamp, 1976 : 25–29, fig. 5, pl. 1, fig. 4; 1979 : 12, pl. 1, figs 1–3.

Luidia marcgravii Steenstrup *in* Lütken, 1859 : 43–46; Verrill, 1915 : 208–209; Boone, 1933 : 76, pls 33–36; Bernasconi, 1958 : 125–127.

Remarks. A very large specimen from *Pillsbury* st. 750, off Venezuela, 22–26 metres with R up to 252 mm may provide a size record.

This locally common caribbean species with its numerous and particularly attenuated arms seems even more vulnerable than most Luidias to loss and regeneration of the arm tips, probably due to predation, possibly cannibalism.

Distribution. Sporadically in southern Florida and from Jamaica eastwards along the Antilles, also Belize and Nicaragua and along the north coast of South America to southern Brazil (Santa Caterina, *c.* 27° S); the original record from Senegal has never been repeated; the records from Belize and Nicaragua are new and derived from the *Pillsbury* collections; 1–64 metres, the depth range also being extended by a *Pillsbury* station (745, off Venezuela, *c.* 12° N, 67° W); the previous maximum depth was 45 m off French Guíana.

Summary of taxonomic changes

The number of nominal Atlantic species of *Luidia* is reduced by the present study from a one-time maximum of 17 to 11.

Luidia aciculata Mortensen, 1933*b* is retained as a subspecies of the Indo-West Pacific *L. sagamina* Döderlein, 1920.

L. africana Sladen, 1889 is reduced to a subspecies of *L. sarsi* Düben & Koren, 1845.

L. barimae John & Clark, 1954 is reduced to a subspecies of *L. heterozona* Fisher, 1940.

L. bernasconiae A. H. Clark, 1945 is again synonymized with *L. alternata* (Say, 1825), having been revived by Gray, Downey & Cerame-Vivas, 1968.

L. elegans Perrier, 1875 is reduced to a subspecies of *L. sarsi.*

L. numidica Koehler, 1911 is treated as a subspecies of *L. alternata.*

L. quequenensis Bernasconi, 1942 is synonymized with *L. alternata.*

L. rosaurae John & Clark, 1954 is synonymized with *L. scotti* Bell, 1917, which is treated as a subspecies of the East Pacific *L. ludwigi* Fisher, 1906.

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References

Bell, F. J. 1893. *Catalogue of the British Echinoderms in the British Museum (Natural History).* London xvii + 202 pp., 16 pls.

—— 1917. Echinoderma. 1. Actinogonidiata. *Brit. Antarct. (Terra Nova) Exped.* 1910. Zool. **4** (1): 1–10, 2 pls.

Bernasconi, I. 1941. Dos nuevas especies argentinas de "*Luidia*". *Physis, B. Aires* **19** : 117–118.

—— 1942. Los Asteroideos sudamericanos de la familia "Luidiidae". *Physis, B. Aires* **19** : 252–253.

—— 1943. Los Asteroideos sudamericanos de la familia Luidiidae. *An. Mus. argent, B. Aires* **41** : 1–20, 5 pls.

—— 1958. Equinoideos y asteroideos de la collección del Instituto Oceanografico de la Universidad de San Pablo. 2. *Bol. Inst. oceanogr. S. Paulo* 7 : 119–149, 4 pls.

—— 1960. Los equinodermos de la campaña 1958 del buque oceanográfico *Capitán Cánepa* A.R.A. *Actas Trab. I Congr. sudamer. Zool.*, 1959. **2** : 21–32, 3 pls.

Blake, D. B. 1973. Ossicle morphology of some recent asteroids and description of some west American fossil asteroids. *Univ. Calif. Publs geol. Sci.* **104** : 1–59, 3 figs, 19 pls.

—— 1982. Somasteroidea, Asteroidea and the affinities of *Luidia (Platasterias) latiradiata* (Gray), 1840, *Palaeontology* **25** : 167–191.

Boone, L. 1933. Coelenterata, Echinodermata and Mollusca. *Bull Vanderbilt mar. Mus.* **4** : 1–217, 133 pls.

Cadenat, J. 1941. Les Echinodermes de la cote occidentale d'Afrique. Description d'une astérie nouvelle de la région du Cap Blanc. *Ann. Soc. Sci nat. Charente Inf.* N.S. **3** : 53–67, 3 figs.

Carrera-Rodriguez, C. J. & Tommasi, L. R. 1977. Asteroidea de la plataforma continental de Rio Grande do Sul (Brasil). *Bolm Inst. oceanogr. S. Paulo* **26** (1) : 51–130, 33 figs.

Cherbonnier, G. 1959. Echinodermes de la Guyane française. 2. *Bull. Mus. natn. Hist. nat. Paris* **31** : 168–172, figs 3, 4.

—— 1963. Echinodermes des côtes du Cameroun récoltés par A. Crosnier. *Bull. Mus. natn. Hist. nat. Paris* **35** : 179–193, 3 figs.

Clark, A. H. 1945. A new starfish of the genus *Luidia* from the coast of Georgia. *J. Wash. Acad. Sci.* **35** : 19–21.

—— 1954. Echinoderms (other than holothurians) of the Gulf of Mexico. *Bull. U.S. Fish. Commn* **55** : 373–379.

Clark, A. M. 1952. Some echinoderms from South Africa. *Trans. R. Soc. S. Afr.* **33** : 193–221, 3 figs, 1 pl.

—— 1953. Notes on asteroids in the British Museum (Natural History). 3. *Luidia*. 4. *Tosia* and *Pentagonaster*. *Bull. Br. Mus. nat. Hist.* Zool. **1** : 379–412, 15 figs, 8 pls.

—— 1955. Echinodermata of the Gold Coast. *Jl W. Afr. Sci. Assn* **1** : 16–56, 23 figs, 1 pl.

—— 1977. The South African Museum's *Meiring Naude* cruises. 4. Echinoderms. *Annls S. Afr. Mus.* **73** : 133–147.

Clark, A. M. & Courtman-Stock, J. 1976. *The echinoderms of southern Africa*. Publs Br. Mus. nat. Hist. No. 776, 277 pp., 276 figs.

Clark, H. L. 1923. The echinoderm fauna of South Africa. *Annls S. Afr. Mus.* **13** : 221–435, 4 figs, 6 pls.

—— 1933. A handbook of the littoral echinoderms of Porto Rico and the other West Indian islands. *Scient. Surv. P. Rico* **16** : 1–147, 7 pls.

—— 1941. Reports on the scientific results of the *Atlantis* Expeditions to the West Indies. The echinoderms. *Mem. Soc. cubana Hist. nat.* **15** : 1–54, 10 pls.

Döderlein, L. 1920. Die Asteriden der Siboga-Expedition. 2. Die Gattung *Luidia* und ihre stammesgeschichte. *Siboga Exped.* **46b** : 193–291, 5 figs, 3 pls.

Downey, M. E. 1973. Starfishes from the Caribbean and the Gulf of Mexico. *Smithson. Contr. Zool.* No. 126 : 1–158, 48 pls.

Düben, M. W. von (& Koren, J.) 1845. Norriges Hafs-fauna. *Ofvers. K. VetenskAkad Förh.* **1844** : 110–116.

—— 1846. Öfversigt af Skandinaviens Echinodermer. *K. svenska VetenskAkad. Handl.* **1844** : 229–328, 6 pls.

Engel, H., Croes, A. F. & Schroevers, G. F. 1960. Les Astérides recoltées par l'expedition du navire-école belge *Mercator*, 1935–36. A. Les Astérides recoltées sur les côtes orientales de l'Amerique entre la Floride et la Vénézuela. (Engel & Schroevers). B. Les Astérides de la côte occidentale d'Afrique. (Engel & Croes). *Bull. Inst. roy. Sci. nat. Belg.* **36** (54) : 1–10; 10–15, 6 pls.

Fell, H. B. 1963. The phylogeny of sea-stars. *Phil. Trans.* **246B** : 381–435, 2 pls.

Fisher, W. K. 1911. Asteroidea of the North Pacific and adjacent waters. *Bull. U.S. natn. Mus.* **76** (1) : 1–419, 122 pls.

—— 1940. Asteroidea. '*Discovery*' *Rep.* **20** : 69–316, 23 pls.

Forbes, E. 1839. On the Asteriadae of the Irish Sea. *Mem. Wernerian nat. Hist. Soc.* **8** : 113–130, 2 pls.

—— 1841. *A history of british starfishes and other animals of the class Echinodermata.* xx + 270 pp., figs. London.

Gray, I. E., Downey, M. E. & Cerame-Vivas, M. J. 1968. Seastars of North Carolina. *Fishery Bull. Fish Wildl. Serv. U.S.* **67** : 127–163, 40 figs.

Gray, J. E. 1840. A synopsis of the genera and species of the class Hypostoma (*Asterias*, Linn.) *Ann. Mag. nat. Hist.* **6** : 175–184; 275–290.

Jangoux, M. 1975. Note sur le genre *Tethyaster* Sladen (Echinodermata, Asteroidea). *Revue zool. afr.* **89** (4) : 761–768, 4 figs.

—— 1978. Les étoiles de mer (Echinodermata: Asteroidea) récoltées par le M/V *Calamar* au large des Guyanes et du Venezuela. *Bull. zool. Mus. Univ. Amsterdam* **6** (13) : 93–101, 3 figs.

John, D. D. & Clark, A. M. 1954. The "Rosaura" Expedition. 3. Echinodermata. *Bull. Br. Mus. nat. Hist.* Zool. **2** (6) : 139–162, 12 figs, 1 pl.

Koehler, R. 1895. Notes Echinologiques. *Revue biol. N. Fr.* **7** : 317–342, 1 pl.

—— 1909. Echinodermes provenant des campagnes du yacht *Princesse-Alice. Result. Camp. scient. Prince Albert* **34** : 1–317, 32 pls.
—— 1911. Mission Gruvel sur la côte occidentale d'Afrique. Echinodermes. *Annls Inst. océanogr. Monaco* **2** (5) : 1–25, 3 pls.
—— 1914. Asteroidea, Ophiuroidea et Echinoidea. *Beitr. Kennt. Meeresfauna Westafr.* **1** (2) : 129–303, 12 pls.
—— 1921. Echinodermes. *Faune Fr.* **1** : 1–210, 153 figs.
—— 1923. Astéries et Ophiures recueillis par l'expedition antarctique suédoise 1901–03. *Further zool. Results Swed. Antarct. Exped.* **1** (1) : 1–145, 1 fig., 15 pls.
Lamarck, J. B. P. A. de 1816. *Histoire naturelle des animaux sans vertèbres.* Ed. 1. **2:** 522–568; **3** : 1–59; 60–76. Paris.
Linnaeus, C. 1758. *Systema Naturae.* Ed. 10. **1** : 824 pp. Holmiae.
Ludwig, H. 1897. Die Seesterne des Mittelmeeres. *Fauna Flora Golf. Neapel* **24** : 1–491, 12 pls.
Lütken, C. 1859. Bidrag til Kundskab om de ved Kysterne af Mellem- og Syd-America levende arter af Söstjerner. *Vidensk. Meddr dansk. naturh. Foren.* **1859** : 25–96.
McKnight, D. G. 1977. Classification of recent paxillosid sea-stars (Asterozoa: Echinodermata). *NZOI Rec.* **3** (12) : 113–119, figs.
Madsen, F. J. 1950. The echinoderms collected by the *Atlantide* Expedition, 1945–46. 1. Asteroidea. *Atlantide Rep.* **1** : 167–222, 11 figs, 3 pls.
Marenzeller, E. von 1893. Veröffentlichungen der Commission für Enforschung des östlichen Mittelmeeres. *Sber. Akad. Wiss. Wien* Math. naturw. Kl. **102** : 1–5.
Mortensen, T. 1925. Echinodermes du Maroc et de Mauritanie. *Bull. Soc. Sci. nat. Maroc* **5** : 178–187, 1 pl.
—— 1927. *Handbook of the Echinoderms of the British Isles.* ix + 471 pp., 269 figs. London.
—— 1933*a*. Echinoderms of South Africa (Asteroidea and Ophiuroidea). *Vidensk. Meddr dansk naturh. Foren.* **93** : 215–400, 91 figs, 12 pls.
—— 1933*b*. The echinoderms of St Helena. *Vidensk. Meddr dansk naturh. Foren.* **93** : 401–472, 29 figs, 3 pls.
Müller, J. & Troschel, F. H. 1840. *Mber. Akad. Wiss. Berlin* **1840** : 100–106.
—— 1842. *System der Asteriden.* 1. Asteriae. 2. Ophiuridae. xx + 134 pp., 12 pls. Braunschweig.
Nataf, G. & Cherbonnier, G. 1973. Les astérides d'Afrique occidentale, utilisation du microscope électronique à balayage pour étude systématique des *Luidia. Bull. Mus. natn. Hist. nat. Paris* (Zool) No. 81 : 69–101, 9 pls.
Pennant, T. 1777. *British Zoology.* Ed. 4. **4** : 1–154, 93 pls. London.
Perrier, E. 1869. *Recherches sur les Pédicellaires et les Ambulacres des Astéries et les Oursins.* 188 pp., 2 pls. Paris [Also in *Annls Sci. nat.* **12**[1869] : 197–304; **13**[1870] : 1–81.]
—— 1875. *Révision de la collection de Stellérides du Museum d'Histoire Naturelle de Paris.* 384 pp. Paris. [Also in *Archs Zool. exp. gén.* **4**[1875] : 265–450; **5**[1876] : 1–104; 209–309.]
—— 1881. Description sommaire des espèces nouvelles d'Astéries. *Bull. Mus. comp. Zool. Harv.* **9** : 1–31.
—— 1882. *In*: Milne Edwards, A. Rapport sur les traveaux de la Commission chargée par M. le ministre de l'Instruction publique d'étudier la faune sous-marine dans le grandes profundeurs de la Méditerranée et de l'Atlantique. (Echinodermes). *Arch. Missions sci. litt: Rapp. et Instr.* ser 3, **9** : 46–49, fig.
—— 1884. Mémoire sur les Etoiles de Mer recueillies dans la Mer des Antilles et le Golfe de Mexique. *Nouv. Archs Mus. Hist. nat. Paris* (2) **6** : 127–276, 10 pls.
—— 1894. Stellerides. *Expéd. scient. Travailleur-Talisman.* 431 pp., 26 pls. Paris.
Philippi, R. 1837. Ueber die mit *Asterias aurantiaca* verwandten und verwechselten Asterian der sicilianischen Küste. *Arch. Naturgesch.* **3** : 193–194.
Sars, M. 1835. Radiater. *Beskrivelser og Jagttagelser over nogle märkelige eller nye i Havet ved den Bergenske Kyst levende Dyr.* pp. 39–46. Bergen.
Say, T. 1825. On the species of the Linnaean genus *Asterias* inhabiting the coast of the United States. *J. Acad. nat. Sci. Philad.* **5** : 141–154.
Sibuet, M. 1975. Astérides abyssales de l'Atlantique sud. *Bull. Mus. natn. Hist. nat. Paris* (Zool.) No. 199 : 281–296, 2 figs, pl.
Sladen, W. P. 1889. Asteroidea. *Rep. scient. Results Voy. Challenger* Zool. **30** : 1–935, 118 pls.
Spencer, W. K. & Wright, C. W. 1966. Asterozoans. *In*: Moore, R. C. [Ed.] *Treatise on invertebrate paleontology.* U. Echinodermata **3** (1) : 4–107, 89 figs. Geological Society of America Inc.: University of Kansas Press.

Studer, T. 1884. Verzeichniss der während der Reise S.M.S. *Gazelle* um die Erde 1874–76 gessammelten Asteriden und Euryaliden. *Phys. Abh. K. Akad. Wiss. Berlin* [1883, 1884] **3** : 1–64, 5 pls.

Süssbach, S. & Breckner, A. 1911. Die Seeigel, Seesterne und Schlangensterne der Nord- und Ostsee. *Wiss. Meeresunters. Kiel* N.S. **12** : 167–300, 3 pls.

Tattersall, W. M. & Sheppard, E. M. 1934. Observations on the Bipinnaria of the asteroid genus *Luidia*. James Johnstone Memorial Volume: Lancs Sea-Fisheries Laboratory, Liverpool. pp. 35–61, 8 figs.

Tommasi, L. R. 1958. Os equinodermas do litoral de São Paulo. 2. *Contrções avuls. Inst. oceanogr. S. Paulo* No. 2 : 1–27, 6 pls.

—— 1970. Lista dos asteroides recentes do Brasil. *Contrções Inst. oceanogr. Univ. S. Paulo* No. 18 : 1–61, 60 figs.

—— 1974. Equinodermes do Brasil. 3. *Publ. Inst. oceanogr. Univ. S. Paulo* No. 369 : 1–15, 12 figs.

Tortonese, E. 1965. Echinodermata. *Fauna d'Italia*. **6** : xv + 422, 186 figs. Bologna.

Ummels, F. 1963. Asteroids from the Netherlands Antilles and other Caribbean localities. *Stud. Fauna Curaçao* **15** : 72–101, 3 figs, 9 pls. [Also in *Natuurwet. Stud. Suriname* No. 30.]

Ursin, E. 1960. A quantitative investigation of the echinoderm fauna of the central North Sea. *Medd. Danmarks Fisk. Havundersøg.* N.S. **2** (24) : 1–204, 96 figs.

Verrill, A. E. 1885. Results of the explorations made by the steamer *Albatross* off the northern coast of the United States in 1883. *Rep. U.S. Fish. Commn* **1883** : 503–543, pls 13–19.

—— 1899. Revision of certain genera and species of starfishes with descriptions of new forms. *Trans. Conn. Acad. Arts Sci.* **1899** : 145–234, pls 24–30.

—— 1915. Report on the starfishes of the West Indies, Florida and Brazil. *Bull. Labs nat. Hist. St. Univ. Ia* **7** (1) : 1–232, 29 pls.

Walenkamp, J. H. C. 1976. The asteroids of the coastal waters of Surinam. *Zool. Verh. Leiden* No. 147 : 1–91, 16 figs, 18 pls.

—— 1979. Asteroidea (Echinodermata) from the Guyana shelf. *Zool. Verh. Leiden* No. 170 : 1–97, 31 figs, 20 pls.

Zoppi de Roa, E. 1967. Contribucion al estudio de los Equinodermos de Venezuela. *Acta biol. venez.* **5** : 267–333, 29 figs.

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